

TRAIT SUBSTITUTION TREES ON TWO TIME SCALES ANALYSIS

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ABSTRACT. In this paper we consider two continuous-mass population models as analogues of logistic branching random walks, one is supported on a finite trait space and the other one is supported on an infinite trait space. For the first model with nearest-neighbor competition and migration, we justify a well-described evolutionary path to the short-term equilibrium on a slow migration time scale. For the second one with an additional evolutionary mechanism-mutation, a jump process-trait substitution tree model is established under a combination of rare mutation and slow migration limits. The transition rule of the tree highly depends on the relabeled trait sequence determined by the fitness landscape. The novelty of our model is that each trait, which may nearly die out on the migration time scale, has a chance to recover and further to be stabilized on the mutation time scale because of a change in the fitness landscape due to a newly entering mutant.

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1. INTRODUCTION

In recent years a spatially structured population with migration (namely mutation in [3]) and local regulation proposed by Bolker and Pacala [1], Dieckmann and Law [7]

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(BPDL process) has attracted particular interest both from biologists and mathematicians. It has several advantages over the traditional branching processes, which make it more natural as a population model: the quadratic competition term is used to prevent the population size from escaping to infinity, and the mutation term is used to create an alternative trait type of the population for selection. Over the last decade, a lot of work has been addressing different aspects on this model. For instance, Etheridge [9], Fournier and Méléard [10], and Hutzenthaler and Wakolbinger [14] study the extinction and survival problems. Champagnat [3], Champagnat and Lambert [4], Champagnat and Méléard [5], Méléard and Tran [16], Dawson and Greven [6] mainly focus on its long time behavior by multi-scale analysis methods.

The present work is largely motivated by the derivation of macroscopic phenomena on the level of populations from the individual based models in the joint limits of large population size and small mutation rates. We mention in particular the work of Fournier and Méléard [10], Champagnat [3] where under certain conditions convergence to the so-called “trait substitution sequence (TSS)” was obtained. More recently, this type of results was extended in Champagnat and Méléard [5] to include further evolutionary phenomena such as evolutionary branching. A common feature of these works is the following setup: one assumes that mutations rates are so small that a monomorphic population, after a single mutation event has sufficient time to move to a new equilibrium where either the mutant trait gets extinct or the mutant trait fixated and the resident trait gets extinct. In this way, one obtains, on the time scale at which such rare mutations occur, a sequence of populations evolving towards increasing fitness, the so-called *trait substitution sequence*. In certain singular situations, one may also reach an equilibrium with co-existing traits, leading to the above-mentioned phenomenon of evolutionary branching [5].

What we wish to add to this picture in the present paper is a more complex structure of populations. The general idea is to consider populations with multiple traits where individual may change (upon birth or otherwise) between a *finite* set of traits at a given (population size independent) rate. We will term such switches “migrations”. In addition, there are *rare* mutations where an individual can be born with a *new* trait which has never been existing in the population.

This set-up is motivated from ideas that are currently discussed intensely in cancer research. The *migration* events can be interpreted as epigenetic switch in the gene-expression of a cell between a variety of possible “metastable” state (see e.g. Huang [13] and Gillies et al [11] and references therein). Mutations are then true mutations that lead to a change in the epigenetically accessible trait-space. See also Hölzel et al for a discussion in the context of cancer evolution [12]. In this paper we consider a very simple caricature of such a complex situations. Our purpose here is limited to showing that such models are still accessible to the mathematical methods developed in recent years, and that such systems give rise to new and interesting mathematical structures.

In this paper we investigate the long term behavior in a two-step limiting procedure where we first let the population size tend to infinity, and then let the migration rate tend to zero while rescaling time in an appropriate way to obtain a non-trivial limit. For a finite trait space, specific conditions are imposed on the fitness and demographic parameters, and a well-described evolutionary path to approach the short-term equilibrium will be obtained on an appropriate time scale. The noteworthy feature here is that these equilibria

can be polymorphic. We call this process a *trait substitution tree (TST)* on the finite trait space. For any given sequence of traits, the equilibrium configuration is determined by their labeled order according to their fitness landscape.

In a second step, we add random mutations on a longer time scale. This is modeled here as the appearance of mass at hitherto unoccupied locations in trait space driven by some Poisson process. The effect of the appearance of such new mass is a reshuffling of the migration part of the process that ends in a new equilibrium configuration. As this process continues, we obtain what we call the *trait substitution tree (TST)* process on infinite state space. The somewhat artificial introduction for mutations in the infinite population model is motivated on the basis of a limit of a finite population model with migration and mutation rates at distinct time scales. Such a model is studied in a companion paper [2].

The remainder of the paper is organized as follows. In Section 2, we briefly describe the microscopic model and give some preliminary results. In particular, we recall the law of large numbers of the BPDL processes. In Section 3, as ϵ tends to 0, on a finite trait space we retrieve a well-defined short-term evolution path to its TST configuration on the migration time scale $O(\ln \frac{1}{\epsilon})$. In Section 4, under the rare mutation constraint we obtain a jump-type TST process on a longer time scale—the mutation time scale. In Section 5, we provide proofs of the results in Section 3 and Section 4. Finally, for better understanding the TST process we provide a simulation algorithm in Section 6.

2. MICROSCOPIC MODEL

2.1. Notation and description of the processes. Following [1], we assume the population at time t is composed of a finite number $I(t)$ of individuals characterized by their phenotypic traits $x_1(t), \dots, x_{I(t)}(t)$ taking values (which can be equal) in a compact subset \mathcal{X} of \mathbb{R}^d .

We denote by $\mathcal{M}_F(\mathcal{X})$ the set of non-negative finite measures on \mathcal{X} . Let $\mathcal{M}_a(\mathcal{X}) \subset \mathcal{M}_F(\mathcal{X})$ be the set of atomic measures on \mathcal{X} :

$$\mathcal{M}_a(\mathcal{X}) = \left\{ \sum_{i=1}^n \delta_{x_i} : x_1, \dots, x_n \in \mathcal{X}, n \in \mathbb{N} \right\}.$$

Then the population process can be represented as:

$$\nu_t = \sum_{i=1}^{I(t)} \delta_{X_i(t)}.$$

Let $B(\mathcal{X})$ denote the totality of bounded and measurable functions on \mathcal{X} . Let $B(\mathcal{M}_F(\mathcal{X}))$ (and $B(\mathcal{M}_a(\mathcal{X}))$) be totality of bounded and measurable functions on $\mathcal{M}_F(\mathcal{X})$ (and $\mathcal{M}_a(\mathcal{X})$). For $\nu \in \mathcal{M}_F(\mathcal{X})$ and $\phi \in B(\mathcal{X})$, denote by $\langle \nu, \phi \rangle = \int \phi d\nu$.

Let's specify the population processes $(\nu_t^n)_{t>0}$ by introducing a sequence of demographic parameters, for $n \in \mathbb{N}$:

- $b_n(x)$ is the rate of birth from an individual with trait x .
- $d_n(x)$ is the rate of death of an individual with trait x because of “aging”.
- $\alpha_n(x, y)$ is the competition kernel felt by some individual with trait x from another individual with trait y .

- $D_n(x, dy)$ is the children's dispersion law from its mother with trait x . In particular, it can be decomposed into two parts-local birth at location x and a small portion of migration based on birth, i.e.

$$D_n(x, dy) = (1 - \epsilon)1_{x=y} + \epsilon m_n(x, dy)1_{x \neq y}. \quad (2.1)$$

Here, $m_n(x, dy)$ is the transition law for migration, which satisfies

$$\int_{y \in \mathcal{X}} m_n(x, dy) = 1.$$

We will omit the superscript ϵ in D_n in the sequel when this leads no ambiguity.

Fournier and Méléard [10] formulated a pathwise construction of the BPDFL process $\{(\nu_t^n)_{t \geq 0}; n \in \mathbb{N}\}$ in terms of Poisson random measures and justified its infinitesimal generator defined for any $\Phi \in B(\mathcal{M}_a(\mathcal{X}))$:

$$\begin{aligned} L_0^n \Phi(\nu) = & \int_{\mathcal{X}} \nu(dx) \int_{\mathbb{R}^d} [\Phi(\nu + \delta_y) - \Phi(\nu)] b_n(x) D_n(x, dy) \\ & + \int_{\mathcal{X}} \nu(dx) [\Phi(\nu - \delta_x) - \Phi(\nu)] \left[d_n(x) + \int_{\mathcal{X}} \alpha_n(x, y) \nu(dy) \right]. \end{aligned} \quad (2.2)$$

The first term is used to model birth events, while the second term which is nonlinear is interpreted as natural death and competing death.

Instead of studying the original BPDFL processes defined by (2.2), our goal is to study the rescaled processes

$$X_t^n := \frac{\nu_t^n}{n}, \quad t \geq 0 \quad (2.3)$$

since it provides us a macroscopic approximation when we take the large population limits (we will see later, the initial population is proportional to n in some sense). The infinitesimal generator of the rescaled BPDFL process has the following form, for any $\Phi \in B(\mathcal{M}_F(\mathcal{X}))$:

$$\begin{aligned} L^n \Phi(\nu) = & \int_{\mathcal{X}} n \nu(dx) \int_{\mathbb{R}^d} \left[\Phi(\nu + \frac{\delta_y}{n}) - \Phi(\nu) \right] b_n(x) D_n(x, dy) \\ & + \int_{\mathcal{X}} n \nu(dx) \left[\Phi(\nu - \frac{\delta_x}{n}) - \Phi(\nu) \right] \left[d_n(x) + \int_{\mathcal{X}} \alpha_n(x, y) n \nu(dy) \right]. \end{aligned} \quad (2.4)$$

2.2. Preliminary results. Let's denote by (A) the following assumptions:

- (A1) There exist $b(x), d(x), \bar{m}(x) \in B(\mathcal{X})$, $\alpha(x, y) \in B(\mathcal{X} \times \mathcal{X})$ with $\bar{m}(x)$ a probability density for $x, y \in \mathcal{X}$, $n \in \mathbb{N}$, such that

$$0 < b_n(x) \equiv b(x), \quad 0 < d_n(x) \equiv d(x), \quad m_n(x, y) \leq \bar{m}(y),$$

$$0 \leq \alpha_n(x, y) = \frac{\alpha(x, y)}{n}$$

- (A2) $b(x) - d(x) > 0$.

The first assumption implies that there exist constants $\bar{b}, \bar{d}, \bar{\alpha}$ such that $b(x) \leq \bar{b}$, $d(x) \leq \bar{d}$, $\alpha(x, y) \leq \bar{\alpha}$. Furthermore, it guarantees the existence of the BPDFL process (see [10]).

By neglecting the high order moment, Bolker and Pacala [1] use the ‘‘moment closure’’ procedure to approximate the stochastic population processes. As we can see from the

generator formula (2.4), due to the quadratic nonlinear term, it should be enough to set the third order moments to be uniformly bounded and “close” the equation up to second order moment. Then Fournier and Méléard [10] obtain a deterministic measure-valued process in the large population limit.

Theorem 2.1 (Fournier and Méléard [10], convergence to an integro-differential equation). *Under the assumption (A1), consider a sequence of processes $(X_t^n)_{t \geq 0}$ defined in (2.3). Suppose that (X_0^n) converges in law to some deterministic finite measure $X_0 \in \mathcal{M}_F(\mathcal{X})$ as $n \rightarrow \infty$ and satisfies $\sup_{n \geq 1} \mathbb{E} \langle X_0^n, 1 \rangle^3 < \infty$. Then the sequence of processes $(X_t^n)_{t \geq 0}$ converges in law as $n \rightarrow \infty$, on $D([0, \infty), \mathcal{M}_F(\mathcal{X}))$, to a deterministic measure-valued process $(X_t)_{t \geq 0} \in C([0, \infty), \mathcal{M}_F(\mathcal{X}))$, where $(X_t)_{t \geq 0}$ is the unique solution satisfying*

$$\sup_{t \in [0, T]} \langle X_t, 1 \rangle < \infty, \quad (2.5)$$

and for any $\phi \in B(\mathcal{X})$,

$$\begin{aligned} \langle X_t, \phi \rangle = & \langle X_0, \phi \rangle + \int_0^t ds \int_{\mathcal{X}} X_s(dx) b(x) \int_{\mathbb{R}^d} \phi(y) D(x, dy) \\ & - \int_0^t ds \int_{\mathcal{X}} X_s(dx) \phi(x) \left[d(x) + \int_{\mathcal{X}} \alpha(x, y) X_s(dy) \right]. \end{aligned} \quad (2.6)$$

3. TST ON A FINITE TRAIT SPACE: WITHOUT MUTATION

The trait substitution sequence (TSS) model is a powerful tool in understanding various evolutionary phenomena, such as evolutionary branching which may lead to speciation (see Champagnat and Méléard [5]). Moreover, the population follows the “hill climbing” process on the increasing fitness landscape, and holds monomorphic trait on a long time scale. This model is proposed by Metz et al. [17] (so called “invasion implies fixation”) and mathematically studied by Champagnat et al. [3, 4, 16].

Notice that the dispersal kernel $D(x, dz)$ implicitly depends on a parameter ϵ (see (2.1)). Rather than taking large population and rare migration limits simultaneously as in [3], we justify a so-called trait substitution tree (TST) from a macroscopic point of view. More precisely, we first consider the large population limit to attain a macroscopic approximation of the individual-based model (see Theorem 2.1). Then, we consider the slow migration limit by a rescaling procedure based on the macroscopic limit. In contrast to the model in Champagnat [3], the migration rate here is not constrained in terms of the demographic parameter (population size).

Here, the so-called TST process arises under the slow migration limit when we assume the nearest-neighbor competition. Note that a variety of short-term evolution paths can be attained by specifying different competition strengths. In other words, the order of invasion and recovery has no special significance even though in this section we restrict the picture by forward invasion into the fitter direction and backward recovery into the unfit direction along the fitness landscape. However, these paths are indistinguishable on a longer scale-the mutation time scale followed by the next section. Nevertheless, apart from the interesting tree structure the TST model also brings us some insights into speciation phenomena - evolution from a monomorphic ancestor to diverse species.

Denote by (C) the following assumptions:

- (C1) Assume $\mathcal{X} = \{x_0, x_1, x_2, \dots, x_L\}$ comprised of distinct traits with index up to $L \in \mathbb{N}$. Monomorphic initial trait: $X_0^n = \frac{N_0^n}{n} \delta_{x_0}$, and $\frac{N_0^n}{n} \xrightarrow{\text{law}} \bar{\xi}(x_0)$ as $n \rightarrow \infty$.
 (C2) Nearest-neighbor competition and migration: $\alpha(x_i, x_j) = m(x_i, x_j) \equiv 0$ for $|i-j| > 1$, and

$$x_0 \prec x_1 \prec \dots \prec x_{L-1} \prec x_L \quad (3.1)$$

where $x_{i-1} \prec x_i$ means $f_{i,i-1} > 0, f_{i-1,i} < 0$ for any $1 \leq i \leq L$ with fitness function $f_{i,j} := b(x_i) - d(x_i) - \alpha(x_i, x_j) \bar{\xi}(x_j)$, and $\bar{\xi}(x_j) := \frac{b(x_j) - d(x_j)}{\alpha(x_j, x_j)}$.

- (C3) For any $i \geq 2$,

$$\frac{i}{b(x_i) - d(x_i)} \geq \frac{1}{f_{i,i-1}} + \frac{1}{f_{i-1,i-2}} + \dots + \frac{1}{f_{1,0}}. \quad (3.2)$$

- (C4) For any $i \geq 0$, $\frac{|f_{i,i+1}|}{f_{i+2,i+1}} < 1$, and

$$\frac{|f_{i,i+1}|}{f_{i+2,i+1}(b(x_i) - d(x_i))} - \frac{1}{f_{i+3,i+2}} > \frac{|f_{i+1,i+2}|}{f_{i+3,i+2}(b(x_{i+1}) - d(x_{i+1}))}. \quad (3.3)$$

Notice that (C3-C4) are just technical assumptions for results in this section but not necessary for results in next section. In fact, assumption (C3) guarantees that the pattern for fixation of fitter traits is in a form of one-by-one replacements until the fittest trait rather than immediate establishments (see proof of Proposition 5.2 and Proposition 5.3). (C4) implies that the recovery time of trait x_i is later than that of type x_{i+1} (see Lemma 5.4).

We first consider the macroscopic limit (2.6) which involves the parameter $\epsilon > 0$, and rewrite it in another form, for any $\phi \in B(\mathcal{X})$,

$$\begin{aligned} \langle X_t^\epsilon, \phi \rangle = & \langle X_0, \phi \rangle + \epsilon \int_0^t ds \int_{\mathcal{X}} X_s^\epsilon(dx) b(x) \int_{\mathcal{X}} [\phi(y) - \phi(x)] m(x, dy) \\ & + \int_0^t ds \int_{\mathcal{X}} X_s^\epsilon(dx) \phi(x) \left[b(x) - d(x) - \int_{\mathcal{X}} \alpha(x, y) X_s^\epsilon(dy) \right]. \end{aligned} \quad (3.4)$$

Suppose that the process is supported on a finite trait space

$$\mathcal{X} = \{x_0, x_1, \dots, x_L\},$$

and allow only nearest-neighbour competition and migration. The infinite population size limit then yields a dynamical system given by

$$\begin{aligned} \xi_t(x_i) = & \xi_0(x_i) + \int_0^t \left[b(x_i) - d(x_i) - \sum_{j=i\pm 1, i} \alpha(x_i, x_j) \xi_s(x_j) \right] \xi_s(x_i) ds \\ & + \epsilon \int_0^t \sum_{j=i\pm 1} [b(x_j) \xi_s(x_j) m(x_j, x_i) - b(x_i) \xi_s(x_i) m(x_i, x_j)] ds, \quad 1 \leq i \leq L. \end{aligned} \quad (3.5)$$

Global existence and uniqueness of the processes follows from Theorem 2.1.

In the following theorem, we derive a trait substitution tree model based on the above macroscopic approximation by letting ϵ tend to zero while rescaling time.

Theorem 3.1. *Admit assumptions (A) and (C), consider the deterministic measure-valued processes $(X_t^\epsilon)_{t \geq 0}$ specified by (3.5) on the trait space $\mathcal{X} = \{x_0, x_1, x_2, \dots, x_L\}$, for any $L \in \mathbb{N}$. Then the sequence of rescaled processes $\left(X_{t \cdot \ln \frac{1}{\epsilon}}^\epsilon\right)_{t \geq 0}$ converges, as $\epsilon \rightarrow 0$, to $(U_t)_{t \geq 0}$ which has the following forms depending on the integer L is even or odd.*

(i) When $L = 2l$ for some $l \in \mathbb{N} \cup 0$,

$$U_t \equiv \begin{cases} \bar{\xi}(x_0)\delta_{x_0} & \text{for } 0 \leq t \leq I_1, \\ \bar{\xi}(x_k)\delta_{x_k} & \text{for } I_k < t \leq I_{k+1}, \quad k = 1, \dots, L-1, \\ \bar{\xi}(x_L)\delta_{x_L} & \text{for } I_L < t \leq I_L + S_{L-2}, \\ \sum_{i=j}^l \bar{\xi}(x_{2i})\delta_{x_{2i}} & \text{for } I_{2j+2} + S_{2j} < t \leq I_{2j} + S_{2j-2}, \quad j = l-1, \dots, 1, \\ \sum_{i=0}^l \bar{\xi}(x_{2i})\delta_{x_{2i}} & \text{for } t > I_2 + S_0. \end{cases} \quad (3.6)$$

where $I_k = \sum_{i=1}^k \frac{1}{f_{i,i-1}}$, and $S_k = \frac{|f_{k,k+1}|}{f_{k+2,k+1}(b(x_k) - d(x_k))}$.

(ii) When $L = 2l + 1$ for some $l \in \mathbb{N} \cup 0$,

$$U_t \equiv \begin{cases} \bar{\xi}(x_0)\delta_{x_0} & \text{for } 0 \leq t \leq I_1, \\ \bar{\xi}(x_k)\delta_{x_k} & \text{for } I_k < t \leq I_{k+1}, \quad k = 1, \dots, L-1, \\ \bar{\xi}(x_L)\delta_{x_L} & \text{for } I_L < t \leq I_L + S_{L-2}, \\ \sum_{i=j}^{l+1} \bar{\xi}(x_{2i-1})\delta_{x_{2i-1}} & \text{for } I_{2j+1} + S_{2j-1} < t \leq I_{2j-1} + S_{2j-3}, \quad j = l, \dots, 2, \\ \sum_{i=1}^{l+1} \bar{\xi}(x_{2i-1})\delta_{x_{2i-1}} & \text{for } t > I_3 + S_1. \end{cases} \quad (3.7)$$

Remark 3.2. (1) As time passes on, the limiting process $(U_t)_{t \geq 0}$ starts with monomorphic substitutions up to the domination of the fittest trait. Afterwards, the relatively unfit traits start to recover along the fitness decreasing direction. From the fittest trait back to the initial one every second one appears in the limit. For instance, when $\mathcal{X} = \{x_0, x_1, x_2\}$, the stable configuration has support $\{x_0, x_2\}$; when $\mathcal{X} = \{x_0, x_1, x_2, x_3\}$, the stable configuration has support $\{x_1, x_3\}$ (see Figure 1). This is because the competition is restricted between nearest neighbors, and the trait on the right hand side is always fitter than the traits on the left.

(2) The TST process indexed by $L + 2$ can be constructed from the TST process indexed by L by adding a three-type sub-tree on top of it. For instance, it is shown in the Figure 2 that the TST (when $L = 4$) can be constructed from a smaller TST (when $L = 2$) by connecting another excursion consisting of traits $\{x_2, x_3, x_4\}$.

We postpone the proof of the above result to Section 5.1.

4. TST ON AN INFINITE TRAIT SPACE: WITH MUTATION

In Section 3 we analyze a continuous-mass population on a finite trait space defined by equation (3.5). On the way towards its equilibrium configuration, under some restrictive conditions, a deterministic evolutionary picture arises on the slow migration time scale $O(\ln \frac{1}{\epsilon})$.

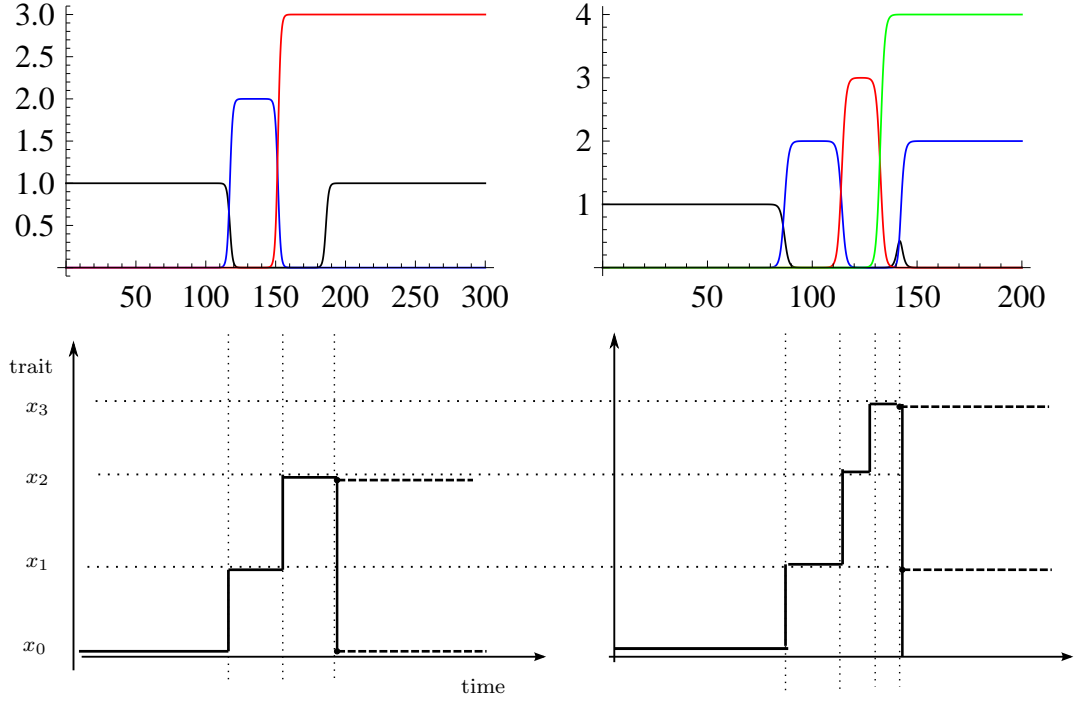


FIGURE 1. Numerical simulations of evolution of a dynamical system with monomorphic initial type and finite trait space (the upper left one has $\mathcal{X} = \{x_0, x_1, x_2\}$ while the upper right one has $\mathcal{X} = \{x_0, x_1, x_2, x_3\}$). Curves describing $\xi_t(x_0), \xi_t(x_1), \xi_t(x_2), \xi_t(x_3)$ are colored black, blue, red, green, resp.. The equilibrium configuration for the first case is $\delta_{x_0} + 3\delta_{x_2}$ and is $2\delta_{x_1} + 4\delta_{x_3}$ for the second one. The lower panel gives their corresponding “trait substitution tree” structure.

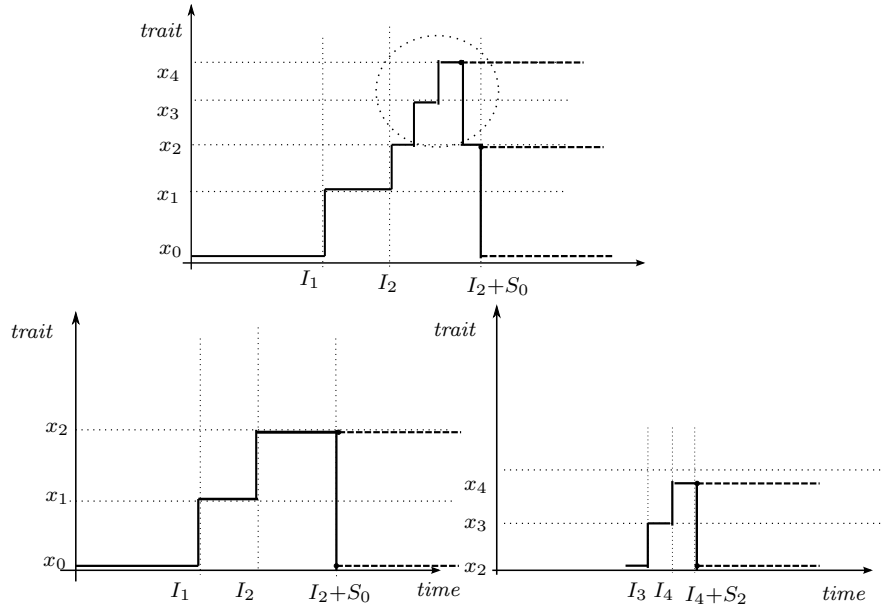


FIGURE 2. Trait substitution tree constructed by embedding excursions.

In order to generalize the process to infinite trait space, we introduce another evolutionary mechanism, mutation of a trait x with a transition kernel $p(x, dh)$ for mutant variation such that $x + h \in \mathcal{X}$. Notice that the essential difference between mutation and migration is that mutation creates some new trait, while migration is only allowed among the existing traits. More precisely, we specify a new model $\{X_t^{\epsilon, \sigma}, t \geq 0\}$ on $D([0, \infty), \mathcal{M}_F(\mathcal{X}))$ with the following infinitesimal generator, for any $\epsilon, \sigma \geq 0$ and proper test functions F and ϕ ,

$$\begin{aligned} L^{\epsilon, \sigma} F(\nu) = & \int_{\mathcal{X}} \left[b(x) - d(x) - \int_{\mathcal{X}} \alpha(x, y) \nu(dy) \right] \frac{\delta F(\nu; x)}{\delta \nu} \nu(dx) \\ & + \epsilon \int_{\mathcal{X}} A\left(\frac{\delta F(\nu; x)}{\delta \nu}\right) \nu(dx) \\ & + \sigma \int_{\mathcal{X}} \int_{\mathbb{R}^d} [F(\nu + \rho \delta_{x+h}) - F(\nu)] \mu(x) p(x, dh) \nu(dx), \end{aligned} \quad (4.1)$$

where the derivative of F is defined by

$$\frac{\delta F(\nu; x)}{\delta \nu} = \lim_{\varepsilon \rightarrow 0+} \frac{F(\nu + \varepsilon \delta_x) - F(\nu)}{\varepsilon} \quad (4.2)$$

and the operator A coincides with the migration term in (3.5)

$$A\phi(x) = \int_{\mathcal{X}} [\phi(y) - \phi(x)] 1_{\{y \in \text{supp}\{\nu\}\}} m(x, dy). \quad (4.3)$$

The first term of the generator describes the local regulation of population dynamics. The second term describes migration among supporting trait sites. Note that migration is not restricted to birth events any more as in (3.5), which is reasonable if we interpret them as a changes in gene expression. The last term creates a new mutant trait to the current population. The mutant mass is specified by a magnitude of $\rho > 0$, which can be taken to zero in a final step. The non-negative function $\mu(x)$ describes the mutation rate of the resident trait x . The parameters ϵ and σ are used to rescale the strength of migration and mutation of the population. For any fixed $\epsilon, \sigma > 0$, the process $\{X_t^{\epsilon, \sigma}, t \geq 0\}$ can be obtained as a large population limit (as $n \rightarrow \infty$) of the processes specified by the generator

$$\begin{aligned} L^{n, \epsilon, \sigma} F(\nu) = & \int_{\mathcal{X}} \left[F(\nu + \frac{\delta_x}{n}) - F(\nu) \right] b(x) n \nu(dx) \\ & + \int_{\mathcal{X}} \left[F(\nu - \frac{\delta_x}{n}) - F(\nu) \right] \left(d(x) + \int_{\mathcal{X}} \alpha(x, y) \nu(dy) \right) n \nu(dx) \\ & + \epsilon \int_{\mathcal{X}} \int_{\mathcal{X}} \left[F(\nu + \frac{\delta_y}{n} - \frac{\delta_x}{n}) - F(\nu) \right] 1_{\{y \in \text{supp}\{\nu\}\}} m(x, dy) n \nu(dx) \\ & + \sigma \int_{\mathcal{X}} \int_{\mathbb{R}^d} [F(\nu + \rho \delta_{x+h}) - F(\nu)] \mu(x) p(x, dh) \nu(dx). \end{aligned} \quad (4.4)$$

For more discussion on discontinuous superprocesses with a general branching mechanism, one can refer to [15]. We will not expand the discussion here.

The following assumptions (D) ensure that the limiting TST process is well-defined.

- (D1) For any given set of distinct traits $\{x_0, x_1, \dots, x_n\} \subset \mathcal{X}$, $n \in \mathbb{N}$, there exists a total order permutation

$$x_{n_0} \prec x_{n_1} \prec \dots \prec x_{n_{n-1}} \prec x_{n_n}, \quad (4.5)$$

where $x \prec y$ means that the fitness functions satisfy $f(x, y) := b(x) - d(x) - \alpha(x, y)\bar{\xi}(y) < 0$, and $f(y, x) := b(y) - d(y) - \alpha(y, x)\bar{\xi}(x) > 0$.

For simplicity, we always assume $x_0^{(n)} \prec x_1^{(n)} \prec \dots \prec x_n^{(n)}$ with $x_i^{(n)} = x_{n_i}$, $1 \leq i \leq n$. Every time a new trait x appears whose fitness is between $x_j^{(n)}$ and $x_{j+1}^{(n)}$ for some $0 \leq j \leq n$, we relabel the traits as follows

$$x_0^{(n+1)} \prec x_1^{(n+1)} \prec \dots \prec x_n^{(n+1)} \prec x_{n+1}^{(n+1)}, \quad (4.6)$$

where $x_i^{(n+1)} = x_i^{(n)}$ for $0 \leq i \leq j$, $x_{j+1}^{(n+1)} = x$ and $x_i^{(n+1)} = x_{i-1}^{(n)}$ for $j+2 \leq i \leq n+1$.

- (D2) Competition and migration only occurs between nearest neighbors, i.e., for totally ordered traits in (D1), we have $m(x_i^{(n)}, x_j^{(n)}) = \alpha(x_i^{(n)}, x_j^{(n)}) \equiv 0$ for $|i - j| > 1$.

Notice that assumptions (C3-C4) provide a convenient setting for which the evolutionary path on the migration time scale can be easily identified. More complex situations can, however, be analyzed in a similar way and lead to qualitatively similar results.

We now give a description of the limiting process on the mutation time-scale.

Definition 4.1. A $\mathcal{M}_F(\mathcal{X})$ -valued Markov jump process $\{\Gamma_t : t \geq 0\}$ characterized as follows is called a trait substitution tree with the ancestor $\Gamma_0 = \bar{\xi}(x_0)\delta_{x_0}$.

- (i) For any non-negative integer l , it jumps from $\Gamma^{(2l)} := \sum_{i=0}^l \bar{\xi}(x_{2i}^{(2l)})\delta_{x_{2i}^{(2l)}}$ to $\Gamma^{(2l+1)}$

with transition rate $\bar{\xi}(x_{2k}^{(2l)})\mu(x_{2k}^{(2l)})p(x_{2k}^{(2l)}, dh)$ for any $0 \leq k \leq l$, where

$$- \Gamma^{(2l+1)} = \sum_{i=1}^j \bar{\xi}(x_{2i-1}^{(2l)})\delta_{x_{2i-1}^{(2l)}} + \bar{\xi}(x_{2k}^{(2l)} + h)\delta_{x_{2k}^{(2l)} + h} + \sum_{i=j+1}^l \bar{\xi}(x_{2i}^{(2l)})\delta_{x_{2i}^{(2l)}}$$

if there exists $0 \leq j \leq l$ s.t. $x_{2j}^{(2l)} \prec x_{2k}^{(2l)} + h \prec x_{2j+1}^{(2l)}$,

$$- \Gamma^{(2l+1)} = \sum_{i=1}^j \bar{\xi}(x_{2i-1}^{(2l)})\delta_{x_{2i-1}^{(2l)}} + \sum_{i=j}^l \bar{\xi}(x_{2i}^{(2l)})\delta_{x_{2i}^{(2l)}}$$

if there exists $0 \leq j \leq l$ s.t. $x_{2j-1}^{(2l)} \prec x_{2k}^{(2l)} + h \prec x_{2j}^{(2l)}$.

Then, we relabel the trait sequence according to the total order relation as in (D1):

$$x_0^{(2l+1)} \prec x_1^{(2l+1)} \prec \dots \prec x_{2l}^{(2l+1)} \prec x_{2l+1}^{(2l+1)}, \quad (4.7)$$

where in associate with the first case

$$x_i^{(2l+1)} := x_i^{(2l)} \text{ for } 0 \leq i \leq 2j, \quad x_{2j+1}^{(2l+1)} := x_{2k}^{(2l)} + h,$$

$$x_i^{(2l+1)} := x_{i-1}^{(2l)} \text{ for } 2j+2 \leq i \leq 2l+1,$$

and in associate with the second case

$$x_i^{(2l+1)} := x_i^{(2l)} \text{ for } 0 \leq i \leq 2j-1, \quad x_{2j}^{(2l+1)} := x_{2k}^{(2l)} + h,$$

$$x_i^{(2l+1)} := x_{i-1}^{(2l)} \text{ for } 2j+1 \leq i \leq 2l+1.$$

(ii) For non-negative integer l , it jumps from $\Gamma^{(2l+1)} := \sum_{i=1}^{l+1} \bar{\xi}(x_{2i-1}^{(2l+1)})\delta_{x_{2i-1}^{(2l+1)}}$ to $\Gamma^{(2l+2)}$ with transition rate $\bar{\xi}(x_{2k-1}^{(2l+1)})\mu(x_{2k-1}^{(2l+1)})p(x_{2k-1}^{(2l+1)}, dh)$ for any $1 \leq k \leq l+1$, where

$$- \Gamma^{(2l+2)} = \sum_{i=1}^j \bar{\xi}(x_{2(i-1)}^{(2l+1)})\delta_{x_{2(i-1)}^{(2l+1)}} + \bar{\xi}(x_{2k-1}^{(2l+1)} + h)\delta_{x_{2k-1}^{(2l+1)} + h} + \sum_{i=j+1}^{l+1} \bar{\xi}(x_{2i-1}^{(2l+1)})\delta_{x_{2i-1}^{(2l+1)}}$$

if there exists $1 \leq j \leq l+1$ s.t. $x_{2j-1}^{(2l+1)} \prec x_{2k-1}^{(2l+1)} + h \prec x_{2j}^{(2l+1)}$,

$$- \Gamma^{(2l+1)} = \sum_{i=1}^j \bar{\xi}(x_{2(i-1)}^{(2l+1)})\delta_{x_{2(i-1)}^{(2l+1)}} + \sum_{i=j}^{l+1} \bar{\xi}(x_{2i-1}^{(2l+1)})\delta_{x_{2i-1}^{(2l+1)}}$$

if there exists $1 \leq j \leq l+1$ s.t. $x_{2j-2}^{(2l+1)} \prec x_{2k-1}^{(2l+1)} + h \prec x_{2j-1}^{(2l+1)}$.

Then, we relabel the trait sequence according to the total order relation as in (D1):

$$x_0^{(2l+2)} \prec x_1^{(2l+2)} \prec \dots \prec x_{2l+1}^{(2l+2)} \prec x_{2l+2}^{(2l+2)}, \quad (4.8)$$

where in the first case

$$x_i^{(2l+2)} := x_i^{(2l+1)} \text{ for } 0 \leq i \leq 2j-1, \quad x_{2j}^{(2l+2)} := x_{2k-1}^{(2l+1)} + h,$$

$$x_i^{(2l+2)} := x_{i-1}^{(2l+1)} \text{ for } 2j+1 \leq i \leq 2l+2,$$

and in the second case

$$x_i^{(2l+2)} := x_i^{(2l+1)} \text{ for } 0 \leq i \leq 2j-2, \quad x_{2j-1}^{(2l+2)} := x_{2k-1}^{(2l+1)} + h,$$

$$x_i^{(2l+2)} := x_{i-1}^{(2l+1)} \text{ for } 2j \leq i \leq 2l+2.$$

Remark 4.2. (see Figure 3). According to the definition, the new configuration is constructed in a way that every second trait gets stabilized when one “looks down” from the fittest trait along the fitness landscape. Once a mutant is inserted between two trait levels (say, i and $i+1$), we relabel all the traits above the mutant’s level. However, the mutation only alters the configuration below the $i+1$ th level and not above. To some extent, the construction here is similar to the look-down idea of Coalescent processes (see [8]).

Theorem 4.3. Admit assumption (A) and (D), and consider processes $\{X_t^{\epsilon, \sigma}, t \geq 0\}$ described by the generator (4.1). Suppose that $X_0^{\epsilon, \sigma} = \xi^\epsilon(x_0)\delta_{x_0}$ and $\xi^\epsilon(x_0) \rightarrow \bar{\xi}(x_0)$ in law and $\rho \rightarrow 0$, as $\epsilon \rightarrow 0$. If it holds that

$$\frac{1}{\sigma} \gg \ln \frac{1}{\epsilon}, \quad (4.9)$$

then $(X_{\frac{t}{\sigma}}^{\epsilon, \sigma})_{t \geq 0}$ converges, as $\epsilon \rightarrow 0$, to the trait substitution tree $(\Gamma_t)_{t \geq 0}$ given in Definition 4.1. Convergence is in the sense of finite dimensional distribution.

We postpone the proof of the above result in Section 5.2.

5. OUTLINE OF PROOFS

5.1. Proof of Theorem 3.1. In this section we present the proofs of the results of Section 3. The main idea behind the proofs is that the migration spreads linearly and the nearest neighbor competitive growth spreads exponentially fast. Before proving Theorem

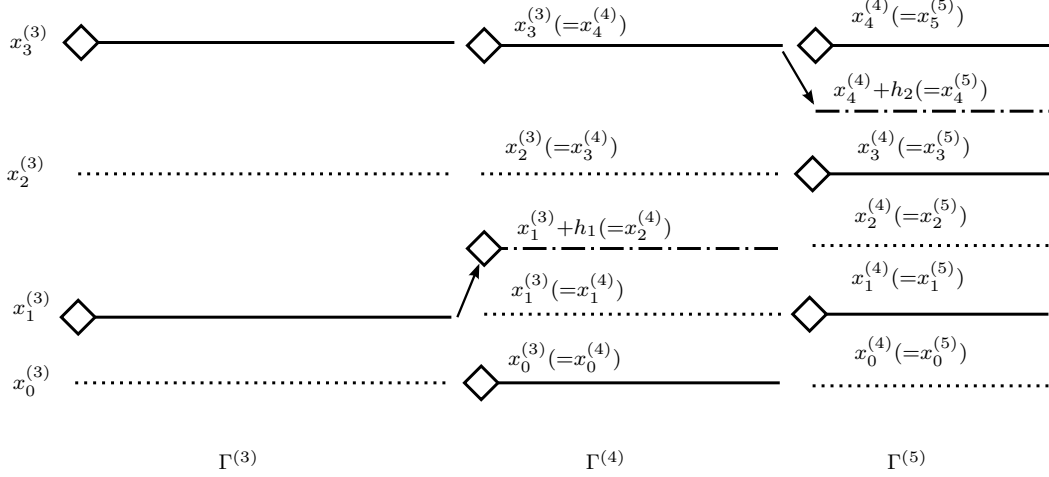


FIGURE 3. A partial path $(\Gamma^{(3)} \rightarrow \Gamma^{(4)} \rightarrow \Gamma^{(5)})$ of the supporting set of the Trait Substitution Tree process defined by Definition 4.1. Solid lines with “diamond” get fixed in the TST process, dotted lines denote virtual traits which are temporarily lost, while dashed lines denote new mutant traits. Arrows denote creation of new mutant types. Starting with state $\Gamma^{(3)}$, the first mutant arises from trait $x_1^{(3)}$, and new trait fits into $x_1^{(3)} \prec x_1^{(3)} + h_1 \prec x_2^{(3)}$. According to Definition 4.1 (ii), traits $x_0^{(3)}$, $x_1^{(3)} + h_1$, $x_3^{(3)}$ get fixed. Consecutively, based on state configuration $\Gamma^{(4)}$, the second mutant arises from trait $x_4^{(4)}$, and new trait fits into $x_3^{(4)} \prec x_4^{(4)} + h_2 \prec x_4^{(4)}$. By Definition 4.1 (i), traits $x_1^{(4)}$, $x_3^{(4)}$, $x_4^{(4)}$ get fixed.

3.1 we state some preliminary results which are key ingredients for the proof of Theorem 3.1.

The following lemma ensures the non-coexistence condition for a dimorphic Lotka-Volterra system. We give the proof in the appendix.

Lemma 5.1. *Consider a dimorphic system*

$$\begin{cases} \dot{\xi}_t(x_i) = \left(b(x_i) - d(x_i) - \alpha(x_i, x_i)\xi_t(x_i) - \alpha(x_i, x_{i+1})\xi_t(x_{i+1}) \right) \xi_t(x_i) \\ \dot{\xi}_t(x_{i+1}) = \left(b(x_{i+1}) - d(x_{i+1}) - \alpha(x_{i+1}, x_i)\xi_t(x_i) - \alpha(x_{i+1}, x_{i+1})\xi_t(x_{i+1}) \right) \xi_t(x_{i+1}), \end{cases} \quad (5.1)$$

with some positive initial condition. If $f_{i,i+1} < 0$, $f_{i+1,i} > 0$, then $(0, \bar{\xi}(x_{i+1}))$ is the only stable equilibrium of (5.1).

The following two propositions are used to prove Theorem 3.1.

Proposition 5.2. *Under the assumptions of Theorem 3.1, for the case when $L = 2$ (i.e. $\mathcal{X} = \{x_0, x_1, x_2\}$), the limit process $(U_t)_{t \geq 0}$ has the form*

$$U_t \equiv \begin{cases} \bar{\xi}(x_0)\delta_{x_0} & \text{for } 0 \leq t \leq I_1, \\ \bar{\xi}(x_1)\delta_{x_1} & \text{for } I_1 < t \leq I_2, \\ \bar{\xi}(x_2)\delta_{x_2} & \text{for } I_2 < t \leq I_2 + S_0, \\ \bar{\xi}(x_0)\delta_{x_0} + \bar{\xi}(x_2)\delta_{x_2} & \text{for } t > I_2 + S_0, \end{cases} \quad (5.2)$$

where $I_1 = \frac{1}{f_{1,0}}$, $I_2 = \frac{1}{f_{1,0}} + \frac{1}{f_{2,1}}$, and $S_0 = \frac{|f_{0,1}|}{f_{2,1}(b(x_0) - d(x_0))}$.

Proof. (a) First, suppose that the population consists of only two types, $\mathcal{X} = \{x_0, x_1\}$. We divide the entire invasion period into four steps, as shown in Figure 4.

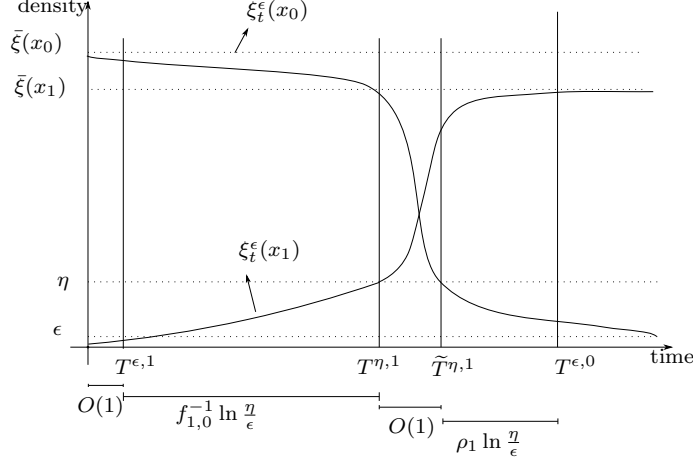


FIGURE 4. Four-step invasion analysis for a dimorphic system

Let $\xi_t^\epsilon(x_0) := \langle X_t^\epsilon, 1_{\{x_0\}} \rangle$ and $\xi_t^\epsilon(x_1) := \langle X_t^\epsilon, 1_{\{x_1\}} \rangle$. From (3.5) one obtains

$$\begin{aligned} \dot{\xi}_t^\epsilon(x_0) = & (b(x_0) - d(x_0) - \alpha(x_0, x_0)\xi_t^\epsilon(x_0) - \alpha(x_0, x_1)\xi_t^\epsilon(x_1))\xi_t^\epsilon(x_0) \\ & - \epsilon\xi_t^\epsilon(x_0)b(x_0)m(x_0, x_1) + \epsilon\xi_t^\epsilon(x_1)b(x_1)m(x_1, x_0), \end{aligned} \quad (5.3)$$

and

$$\begin{aligned} \dot{\xi}_t^\epsilon(x_1) = & (b(x_1) - d(x_1) - \alpha(x_1, x_0)\xi_t^\epsilon(x_0) - \alpha(x_1, x_1)\xi_t^\epsilon(x_1))\xi_t^\epsilon(x_1) \\ & - \epsilon\xi_t^\epsilon(x_1)b(x_1)m(x_1, x_0) + \epsilon\xi_t^\epsilon(x_0)b(x_0)m(x_0, x_1), \end{aligned} \quad (5.4)$$

where $\xi_0^\epsilon(x_0) = \bar{\xi}(x_0)$ and $\xi_0^\epsilon(x_1) = 0$.

Step 1. For any fixed $\eta > 0$, $\forall 0 < \epsilon < \eta$, let $T^{\epsilon,1}$ be the time when $(\xi_t^\epsilon(x_0), \xi_t^\epsilon(x_1))$ leaves the ϵ -neighborhood of $(\bar{\xi}(x_0), 0)$, i.e.

$$T^{\epsilon,1} = \inf \{t \geq 0 : \xi_t^\epsilon(x_1) > \epsilon, \text{ or } \xi_t^\epsilon(x_0) < \bar{\xi}(x_0) - \epsilon\}.$$

From (5.4) it follows that, for $t < T^{\epsilon,1}$, $\xi_t^\epsilon(x_1)$ satisfies the following differential inequality:

$$\begin{aligned} \dot{\xi}_t^\epsilon(x_1) \geq & (b(x_1) - d(x_1) - \alpha(x_1, x_0)\bar{\xi}(x_0) - \epsilon\alpha(x_1, x_1) - \epsilon b(x_1)m(x_1, x_0))\xi_t^\epsilon(x_1) \\ & + \epsilon(\bar{\xi}(x_0) - \epsilon)b(x_0)m(x_0, x_1) \\ = & (f_{1,0} - \epsilon(\alpha(x_1, x_1) + b(x_1)m(x_1, x_0)))\xi_t^\epsilon(x_1) + \epsilon(\bar{\xi}(x_0) - \epsilon)b(x_0)m(x_0, x_1). \end{aligned} \quad (5.5)$$

Since $f_{1,0} = b(x_1) - d(x_1) - \alpha(x_1, x_0)\bar{\xi}(x_0) > 0$, we can choose ϵ sufficiently small so that the first term on the right hand side of the above inequality is positive. Omitting this positive term, one sees that $\dot{\xi}_t(x_1) \leq \xi_t^\epsilon(x_1)$, where $\xi_0(x_1) = 0$, and

$$\dot{\xi}_t(x_1) = \epsilon(\bar{\xi}(x_0) - \epsilon)b(x_0)m(x_0, x_1). \quad (5.6)$$

Thus, $T^{\epsilon,1}$ can be bounded from above by $\tilde{T}^{\epsilon,1} = ((\bar{\xi}(x_0) - \epsilon)b(x_0)m(x_0, x_1))^{-1}$, which is the time when $\xi_t(x_1)$ reaches the level ϵ -level. Thus, $T^{\epsilon,1}$ is of order $O(1)$.

Step 2. After time $T^{\epsilon,1}$, we consider the evolution of the population $(\xi_t^\epsilon(x_0), \xi_t^\epsilon(x_1))$ until the time (denoted by $T^{\eta,1}$) when it leaves the η -neighborhood of $(\bar{\xi}(x_0), 0)$. From (5.4), omitting the term $\epsilon \xi_t^\epsilon(x_0) b(x_0) m(x_0, x_1)$, we get

$$\begin{aligned} \dot{\xi}_t^\epsilon(x_1) &\geq (b(x_1) - d(x_1) - \alpha(x_1, x_0) \xi_t^\epsilon(x_0) - \alpha(x_1, x_1) \xi_t^\epsilon(x_1)) \xi_t^\epsilon(x_1) - \epsilon \xi_t^\epsilon(x_1) b(x_1) m(x_1, x_0) \\ &\geq (b(x_1) - d(x_1) - \alpha(x_1, x_0) \bar{\xi}(x_0) - \eta \alpha(x_1, x_1)) \xi_t^\epsilon(x_1) - \eta \xi_t^\epsilon(x_1) b(x_1) m(x_1, x_0) \\ &= (f_{1,0} - \eta \check{C}) \xi_t^\epsilon(x_1), \end{aligned} \tag{5.7}$$

where $\check{C} = \alpha(x_1, x_1) + b(x_1) m(x_1, x_0)$. On the other hand, by omitting some negative terms in (5.4), we get

$$\begin{aligned} \dot{\xi}_t^\epsilon(x_1) &\leq (b(x_1) - d(x_1) - \alpha(x_1, x_0) \xi_t^\epsilon(x_0)) \xi_t^\epsilon(x_1) + \epsilon \xi_t^\epsilon(x_0) b(x_0) m(x_0, x_1) \\ &\leq (b(x_1) - d(x_1) - \alpha(x_1, x_0) (\bar{\xi}(x_0) - \eta)) \xi_t^\epsilon(x_1) + \epsilon \bar{\xi}(x_0) b(x_0) m(x_0, x_1) \\ &\leq (f_{1,0} + \eta \hat{C}) \xi_t^\epsilon(x_1), \end{aligned} \tag{5.8}$$

where $\hat{C} = \alpha(x_1, x_0) + \bar{\xi}(x_0) b(x_0) m(x_0, x_1)$.

Applying Gronwall's inequality to (5.7) and (5.8), the density $\xi_t^\epsilon(x_1)$, starting with $\xi_{T^{\epsilon,1}}^\epsilon(x_1) = \epsilon$, can be bounded from below by $\check{\xi}_t(x_1)$ and from above by $\hat{\xi}_t(x_1)$, which satisfy the equations

$$\dot{\check{\xi}}_t(x_1) = (f_{1,0} - \check{C} \eta) \check{\xi}_t(x_1), \tag{5.9}$$

and

$$\dot{\hat{\xi}}_t(x_1) = (f_{1,0} + \hat{C} \eta) \hat{\xi}_t(x_1), \tag{5.10}$$

with initial conditions $\check{\xi}_{T^{\epsilon,1}}(x_1) = \hat{\xi}_{T^{\epsilon,1}}(x_1) = \epsilon$, respectively.

The times needed for $\check{\xi}_t(x_1)$ and $\hat{\xi}_t(x_1)$ to reach the η -level can be computed explicitly. They are given by $\check{T}^{\eta,1} - T^{\epsilon,1} = (f_{1,0} - \check{C} \eta)^{-1} \ln \frac{\eta}{\epsilon}$ and $\hat{T}^{\eta,1} - T^{\epsilon,1} = (f_{1,0} + \hat{C} \eta)^{-1} \ln \frac{\eta}{\epsilon}$, respectively. Since $\hat{T}^{\eta,1} < T^{\eta,1} < \check{T}^{\eta,1}$, for any $\eta > 0$, $T^{\eta,1} - T^{\epsilon,1}$ is of order $f_{1,0}^{-1} \ln \frac{1}{\epsilon}$.

Step 3. From (3.5), the process $(\xi_t^\epsilon(x_0), \xi_t^\epsilon(x_1))$ starting from time $T^{\eta,1}$ converges, as $\epsilon \rightarrow 0$, to the solution of the following system:

$$\begin{cases} \dot{\xi}_t(x_0) = (b(x_0) - d(x_0) - \alpha(x_1, x_0) \xi_t(x_0) - \alpha(x_1, x_1) \xi_t(x_1)) \xi_t(x_0) \\ \dot{\xi}_t(x_1) = (b(x_1) - d(x_1) - \alpha(x_1, x_0) \xi_t(x_0) - \alpha(x_1, x_1) \xi_t(x_1)) \xi_t(x_1), \end{cases} \tag{5.11}$$

which has a nontrivial initial value $\xi_{T^{\eta,1}}(x_1) = \eta$, and $\xi_{T^{\eta,1}}(x_0) \in (\bar{\xi}(x_0) - \eta, \bar{\xi}(x_0) + \eta)$. By Lemma 5.1, this dimorphic system has a unique stable equilibrium $(0, \bar{\xi}(x_1))$ under the assumption that $f_{1,0} > 0$, $f_{0,1} < 0$. Let $\tilde{T}^{\eta,1}$ be the time when $(\xi_t^\epsilon(x_0), \xi_t^\epsilon(x_1))$ enters the η -neighborhood of the equilibrium $(0, \bar{\xi}(x_1))$, i.e. $\xi_{\tilde{T}^{\eta,1}}(x_0) = \eta$. Since η is a given fixed constant, $\tilde{T}^{\eta,1} - T^{\eta,1}$ is of order $O(1)$ as $\epsilon \rightarrow 0$.

Step 4. After time $\tilde{T}^{\eta,1}$, we consider the time needed for x_1 to get fixated (i.e. for x_0 gets absorbed at 0). From (5.3), one obtains the differential lower bound:

$$\begin{aligned} \dot{\xi}_t^\epsilon(x_0) &\geq (b(x_0) - d(x_0) - \alpha(x_0, x_0)\xi_t^\epsilon(x_0) - \alpha(x_0, x_1)\xi_t^\epsilon(x_1))\xi_t^\epsilon(x_0) - \epsilon\xi_t^\epsilon(x_0)b(x_0)m(x_0, x_1) \\ &\geq (b(x_0) - d(x_0) - \eta\alpha(x_0, x_0) - \alpha(x_0, x_1)\bar{\xi}(x_1))\xi_t^\epsilon(x_0) - \eta b(x_0)m(x_0, x_1)\xi_t^\epsilon(x_0) \\ &= (f_{0,1} - \eta\check{C})\xi_t^\epsilon(x_0), \end{aligned} \tag{5.12}$$

where $\check{C} = \alpha(x_0, x_0) + b(x_0)m(x_0, x_1)$. As for the upper bound, we observe that

$$\begin{aligned} \dot{\xi}_t^\epsilon(x_0) &\leq (b(x_0) - d(x_0) - \alpha(x_0, x_1)\xi_t^\epsilon(x_1))\xi_t^\epsilon(x_0) + \epsilon\xi_t^\epsilon(x_1)b(x_1)m(x_1, x_0) \\ &\leq (b(x_0) - d(x_0) - \alpha(x_0, x_1)(\bar{\xi}(x_1) - \eta))\xi_t^\epsilon(x_0) + \epsilon\bar{\xi}(x_1)b(x_1)m(x_1, x_0) \\ &\leq (f_{1,0} + \eta\hat{C})\xi_t^\epsilon(x_0), \end{aligned} \tag{5.13}$$

where $\hat{C} = \alpha(x_0, x_1) + \bar{\xi}(x_1)b(x_1)m(x_1, x_0)$.

Applying again Gronwall's inequality to (5.12) and (5.13), we see that $\xi_t^\epsilon(x_0)$, starting with $\xi_{\tilde{T}^{\eta,1}}^\epsilon(x_0) = \eta$, can be bounded from below by $\check{\xi}_t(x_0)$ and from above by $\hat{\xi}_t(x_0)$, which satisfy the equations

$$\dot{\check{\xi}}_t(x_0) = (f_{0,1} - \check{C}\eta)\check{\xi}_t(x_0), \tag{5.14}$$

and

$$\dot{\hat{\xi}}_t(x_0) = (f_{0,1} + \hat{C}\eta)\hat{\xi}_t(x_0), \tag{5.15}$$

with $\check{\xi}_{\tilde{T}^{\eta,1}}(x_0) = \hat{\xi}_{\tilde{T}^{\eta,1}}(x_0) = \eta$.

Since $f_{0,1} = b(x_0) - d(x_0) - \alpha(x_0, x_1)\bar{\xi}(x_1) < 0$, we can choose η small enough so that $f_{0,1} + \hat{C}\eta < 0$. Therefore, both $\check{\xi}_t(x_0)$ and $\hat{\xi}_t(x_0)$ decay exponentially. For any $\rho_1 > 0$, the process $\hat{\xi}_t(x_0)$, in time of order $\rho_1 \ln \frac{\eta}{\epsilon}$, reaches the $\epsilon^{-\rho_1(f_{0,1} + \eta\hat{C})}$ -neighborhood of 0, while $\check{\xi}_t(x_0)$ reaches the $\epsilon^{-\rho_1(f_{0,1} - \eta\check{C})}$ -neighborhood of 0. Let $T^{\epsilon,0} := \tilde{T}^{\eta,1} + \rho_1 \ln \frac{\eta}{\epsilon}$. Then,

$$\begin{aligned} \lim_{\epsilon \rightarrow 0} \hat{\xi}_{T^{\epsilon,0}}^\epsilon(x_0) &= \lim_{\epsilon \rightarrow 0} \hat{\xi}_{\tilde{T}^{\eta,1}}^\epsilon(x_0) \exp\left((f_{0,1} + \hat{C}\eta)(T^{\epsilon,0} - \tilde{T}^{\eta,1})\right) \\ &= \lim_{\epsilon \rightarrow 0} \eta \exp\left((f_{0,1} + \hat{C}\eta) \cdot \rho_1 \log \frac{\eta}{\epsilon}\right) \\ &= \lim_{\epsilon \rightarrow 0} \epsilon^{-\rho_1 f_{0,1}} \cdot O(\eta) \\ &= 0. \end{aligned} \tag{5.16}$$

Similarly, we obtain $\lim_{\epsilon \rightarrow 0} \check{\xi}_{T^{\epsilon,0}}^\epsilon(x_0) = 0$. Therefore, $\lim_{\epsilon \rightarrow 0} \xi_{T^{\epsilon,0}}^\epsilon(x_0) = 0$. Therefore the subpopulation at x_1 eventually gets fixated as $\epsilon \rightarrow 0$.

Combining the four steps above, one concludes that the right time scale for the fitter population x_1 to get fixated is

$$(f_{1,0}^{-1} + \rho_1) \ln \frac{1}{\epsilon}. \tag{5.17}$$

(b) (Recovery process: see Figure 5) Next, we consider the case when there are three distinct trait types, $\mathcal{X} = \{x_0, x_1, x_2\}$. At the same time as the population on the site x_0 migrates towards the new site x_1 (as shown in (a)), the population of trait x_1 can migrate

to the site x_2 . Let $\xi_t^\epsilon(x_2) := \langle X_t^\epsilon, 1_{\{x_2\}} \rangle$. In the following, we re-analyze the evolution process after adding one more trait x_2 to the previous case with trait space $\{x_0, x_1\}$. Due to an ϵ -fraction of initial migration from the subpopulation x_0 to x_1 it follows that a ϵ^2 -fraction migrates from subpopulation x_1 to x_2 . We have $\xi_{T^{\epsilon,1}}^\epsilon(x_2) = \epsilon \xi_{T^{\epsilon,1}}^\epsilon(x_1) = \epsilon^2 \bar{\xi}(x_0)$. Since the population growth of trait x_2 is in an exponential rate $b(x_2) - d(x_2)$, the time needed for $\xi_t^\epsilon(x_2)$, starting with mass of order ϵ^2 to reach the given η -level, is of order $\frac{2}{b(x_2)-d(x_2)} \ln \frac{1}{\epsilon}$.

As shown in Figure 5, because of assumption (C3) we have that $\frac{2}{b(x_2)-d(x_2)} > \frac{1}{f_{1,0}}$, and the influence of the population at x_2 is negligible before the time $T^{\eta,1}$ when the population at x_1 reaches the level η . Since $\tilde{T}^{\eta,1} - T^{\eta,1} = O(1)$, the population at x_2 , starting with $\xi_{\tilde{T}^{\eta,1}}^\epsilon(x_2) = \epsilon \cdot O(1)$, evolves under the competition from its resident population x_1 as follows

$$\begin{aligned} \dot{\xi}_t^\epsilon(x_2) = & (b(x_2) - d(x_2) - \alpha(x_2, x_1)\xi_t^\epsilon(x_1) - \alpha(x_2, x_2)\xi_t^\epsilon(x_2))\xi_t^\epsilon(x_2) \\ & - \epsilon \xi_t^\epsilon(x_2)b(x_2)m(x_2, x_1) + \epsilon \xi_t^\epsilon(x_1)b(x_1)m(x_1, x_2), \end{aligned} \quad (5.18)$$

where $\xi_{\tilde{T}^{\eta,1}}^\epsilon(x_1) \in (\bar{\xi}(x_1) - \eta, \bar{\xi}(x_1) + \eta)$. On the other hand, until time $\tilde{T}^{\eta,1}$ the populations at x_0 and x_1 still behave the same as in Step 1-Step 4. Thus, we embed Figure 4 into Figure 5 and continue the proof based on the four-step analysis in (a).

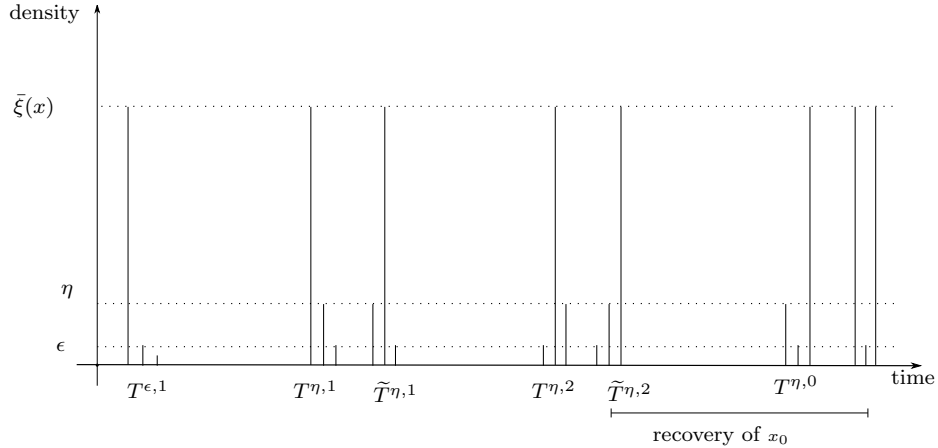


FIGURE 5. Three-type density evolution $(\xi_t^\epsilon(x_0), \xi_t^\epsilon(x_1), \xi_t^\epsilon(x_2))$

Let $T^{\eta,2}$ be the first time when $\xi_t^\epsilon(x_2)$ enters above the level η . By similar arguments as used in Step 2, one can control $\xi_t^\epsilon(x_2)$ by two other curves $\check{\xi}_t(x_2) \leq \xi_t^\epsilon(x_2) \leq \hat{\xi}_t(x_2)$ described as follows, for $\tilde{T}^{\eta,1} < t < T^{\eta,2}$,

$$\dot{\check{\xi}}_t(x_2) = (f_{2,1} - \check{C}\eta)\check{\xi}_t(x_2), \quad (5.19)$$

and

$$\dot{\hat{\xi}}_t(x_2) = (f_{2,1} + \hat{C}\eta)\hat{\xi}_t(x_2), \quad (5.20)$$

where the constants \check{C}, \hat{C} change from line to line and $\check{\xi}_{\tilde{T}^{\eta,1}}(x_2) = \hat{\xi}_{\tilde{T}^{\eta,1}}(x_2) = \epsilon \cdot O(1)$. It follows that

$$\frac{1}{f_{2,1} + \hat{C}\eta} \ln \frac{1}{\epsilon} < T^{\eta,2} - \tilde{T}^{\eta,1} < \frac{1}{f_{2,1} - \check{C}\eta} \ln \frac{1}{\epsilon}. \quad (5.21)$$

On other other hand, due to the comparison assumption (C3): $\frac{2}{b(x_2)-d(x_2)} > \frac{1}{f_{1,0}} + \frac{1}{f_{2,1}}$, we conclude that the shorter time length among the two for $\xi_t^\epsilon(x_2)$ to reach η -level satisfies

$$\left(\frac{1}{f_{1,0}} + \frac{1}{f_{2,1}} - \delta\right) \ln \frac{1}{\epsilon} < T^{\eta,2} < \left(\frac{1}{f_{1,0}} + \frac{1}{f_{2,1}} + \delta\right) \ln \frac{1}{\epsilon}. \quad (5.22)$$

During time interval $[\tilde{T}^{\eta,1}, T^{\eta,2}]$, consider the population $\xi_t^\epsilon(x_0)$. We inherit the estimate $\check{\xi}_t(x_0) < \xi_t^\epsilon(x_0) < \hat{\xi}_t(x_0)$ from Step 4. Subpopulations $\check{\xi}_t(x_0)$ and $\hat{\xi}_t(x_0)$ are described by solutions of two equations (5.14) and (5.15), which imply that

$$\check{\xi}_t(x_0) = \check{\xi}_{\tilde{T}^{\eta,1}}(x_0) e^{(f_{0,1}-\check{C}\eta)(t-\tilde{T}^{\eta,1})}, \quad (5.23)$$

and

$$\hat{\xi}_t(x_0) = \hat{\xi}_{\tilde{T}^{\eta,1}}(x_0) e^{(f_{0,1}+\hat{C}\eta)(t-\tilde{T}^{\eta,1})} \quad (5.24)$$

with $\check{\xi}_{\tilde{T}^{\eta,1}}(x_0) = \hat{\xi}_{\tilde{T}^{\eta,1}}(x_0) = \eta$.

Combining above with (5.21), one obtains

$$\eta \epsilon^{-\frac{f_{0,1}-\check{C}\eta}{f_{2,1}-\check{C}\eta}} < \check{\xi}_{T^{\eta,2}}(x_0) < \xi_{T^{\eta,2}}^\epsilon(x_0) < \hat{\xi}_{T^{\eta,2}}(x_0) < \eta \epsilon^{-\frac{f_{0,1}+\hat{C}\eta}{f_{2,1}+\hat{C}\eta}}. \quad (5.25)$$

Taking ϵ -migration from its neighbor site x_1 into account, the mass on x_0 is of order $\epsilon^{\frac{|f_{0,1}|}{f_{2,1}}} \vee \epsilon$. Due to assumption (C4): $\frac{|f_{0,1}|}{f_{2,1}} < 1$, one obtains that $\epsilon^{\frac{|f_{0,1}|}{f_{2,1}}} \vee \epsilon = \epsilon^{\frac{|f_{0,1}|}{f_{2,1}}}$.

Short after $T^{\eta,2}$, as ϵ tends to 0, there follows an immediate swap between $\xi_t^\epsilon(x_1)$ and $\xi_t^\epsilon(x_2)$ approximated by a Lotka-Volterra system as in Step 3. Denote by $\tilde{T}^{\eta,2}$ the first time when $(\xi_t^\epsilon(x_1), \xi_t^\epsilon(x_2))$ enters the η -neighborhood of the equilibrium $(0, \bar{\xi}(x_2))$, i.e. $\xi_{\tilde{T}^{\eta,2}}^\epsilon(x_1) = \eta$. Also, $\tilde{T}^{\eta,2} - T^{\eta,2}$ is of order $O(1)$. Thus, one obtains

$$\epsilon^{-\frac{f_{0,1}-\check{C}\eta}{f_{2,1}-\check{C}\eta}} \cdot O(\eta) < \xi_{\tilde{T}^{\eta,2}}^\epsilon(x_0) = \xi_{T^{\eta,2}}^\epsilon(x_0) \cdot O(1) < \epsilon^{-\frac{f_{0,1}+\hat{C}\eta}{f_{2,1}+\hat{C}\eta}} \cdot O(\eta). \quad (5.26)$$

Let $T^{\eta,0}$ denote the first time after time $\tilde{T}^{\eta,2}$ when $\xi_t^\epsilon(x_0)$ reaches η -level. For $\tilde{T}^{\eta,2} < t < T^{\eta,0}$, $\xi_t^\epsilon(x_0)$ is governed approximately by a logistic equation

$$\dot{\xi}_t(x_0) = (b(x_0) - d(x_0) - \alpha(x_0, x_0)\xi_t(x_0))\xi_t(x_0). \quad (5.27)$$

Then, we have the differential inequality

$$(b(x_0) - d(x_0) - \alpha(x_0, x_0)\eta)\xi_t(x_0) < \dot{\xi}_t(x_0) < (b(x_0) - d(x_0))\xi_t(x_0), \quad (5.28)$$

where $\xi_{\tilde{T}^{\eta,2}}(x_0)$ satisfies (5.26). Then, by Gronwall's inequality, one obtains

$$\begin{aligned} -\frac{f_{0,1} + \hat{C}\eta}{(f_{2,1} + \hat{C}\eta)(b(x_0) - d(x_0))} \ln \frac{1}{\epsilon} &< T^{\eta,0} - \tilde{T}^{\eta,2} \\ &< -\frac{f_{0,1} - \check{C}\eta}{(f_{2,1} - \check{C}\eta)(b(x_0) - d(x_0) - \alpha(x_0, x_0)\eta)} \ln \frac{1}{\epsilon}. \end{aligned} \quad (5.29)$$

After $T^{\eta,0}$, $\xi_t^\epsilon(x_0)$ approaches $\bar{\xi}(x_0)$ in time length of order 1.

Combining the analysis on $T^{\eta,1}$ in Step 2, and the estimates in (5.21) and (5.29), since $\eta > 0$ is arbitrary, we obtain that

$$\begin{aligned} \lim_{\eta \rightarrow 0} \frac{T^{\eta,1}}{\ln \frac{1}{\epsilon}} &= \frac{1}{f_{1,0}} =: I_1, \\ \lim_{\eta \rightarrow 0} \frac{T^{\eta,2} - \tilde{T}^{\eta,1}}{\ln \frac{1}{\epsilon}} &= \frac{1}{f_{2,1}} =: I_2 - I_1, \\ \lim_{\eta \rightarrow 0} \frac{T^{\eta,0} - \tilde{T}^{\eta,2}}{\ln \frac{1}{\epsilon}} &= \frac{-f_{0,1}}{f_{2,1}(b(x_0) - d(x_0))} =: S_0. \end{aligned} \quad (5.30)$$

Therefore, X_t^ϵ , rescaled on a time scale of order $\ln \frac{1}{\epsilon}$, converges to the TST process U_t ($L = 2$) with the form (5.2). \square

Proposition 5.3. *Admit the same conditions as in Theorem 3.1. Consider the case when $L = 3$, i.e. $\mathcal{X} = \{x_0, x_1, x_2, x_3\}$. Then the limit process $(U_t)_{t \geq 0}$ has the form*

$$U_t \equiv \begin{cases} \bar{\xi}(x_0)\delta_{x_0} & \text{for } 0 \leq t \leq I_1, \\ \bar{\xi}(x_1)\delta_{x_1} & \text{for } I_1 < t \leq I_2, \\ \bar{\xi}(x_2)\delta_{x_2} & \text{for } I_2 < t \leq I_3, \\ \bar{\xi}(x_3)\delta_{x_3} & \text{for } I_3 < t \leq I_3 + S_1, \\ \bar{\xi}(x_1)\delta_{x_1} + \bar{\xi}(x_3)\delta_{x_3} & \text{for } t > I_3 + S_1 \end{cases} \quad (5.31)$$

where $I_3 = \frac{1}{f_{1,0}} + \frac{1}{f_{2,1}} + \frac{1}{f_{3,2}}$, and $S_1 = \frac{|f_{1,2}|}{f_{3,2}(b(x_1) - d(x_1))}$

Proof. (See Figure 6) Due to an ϵ -fraction of migration from a subpopulation to its neighbor subpopulation it follows that $\xi_{T^{\epsilon,1}}^\epsilon(x_3) = \epsilon \xi_{T^{\epsilon,1}}^\epsilon(x_2) = \epsilon^2 \xi_{T^{\epsilon,1}}^\epsilon(x_1) = \epsilon^3 \bar{\xi}(x_0)$. Since the density of trait type x_3 increases in an exponential speed $b(x_3) - d(x_3)$, the time needed to reach a level η -level is of order $\frac{3}{b(x_3) - d(x_3)} \ln \frac{1}{\epsilon}$. By assumption (C3): $\frac{3}{b(x_3) - d(x_3)} > \frac{1}{f_{1,0}} + \frac{1}{f_{2,1}}$, it implies that the population on trait site x_3 is negligible, i.e. of order ϵ , before the time $T^{\eta,2}$. Thus until that time the evolution of the populations at the other sites proceeds as if this site did not exist. The analysis and notations such as $T^{\eta,1}, \tilde{T}^{\eta,1}, T^{\eta,2}, \tilde{T}^{\eta,2}$ then carry over from the proof of Proposition 5.2.

The evolution of $\xi_t^\epsilon(x_3)$ after time $\tilde{T}^{\eta,2}$ is governed by the equation

$$\begin{aligned} \dot{\xi}_t^\epsilon(x_3) &= (b(x_3) - d(x_3) - \alpha(x_3, x_2)\xi_t^\epsilon(x_2) - \alpha(x_3, x_3)\xi_t^\epsilon(x_3))\xi_t^\epsilon(x_3) \\ &\quad - \epsilon \xi_t^\epsilon(x_3)b(x_3)m(x_3, x_2) + \epsilon \xi_t^\epsilon(x_2)b(x_2)m(x_2, x_3), \end{aligned} \quad (5.32)$$

with initial value $\xi_{\tilde{T}^{\eta,2}}^\epsilon(x_3) = \epsilon \cdot O(1)$.

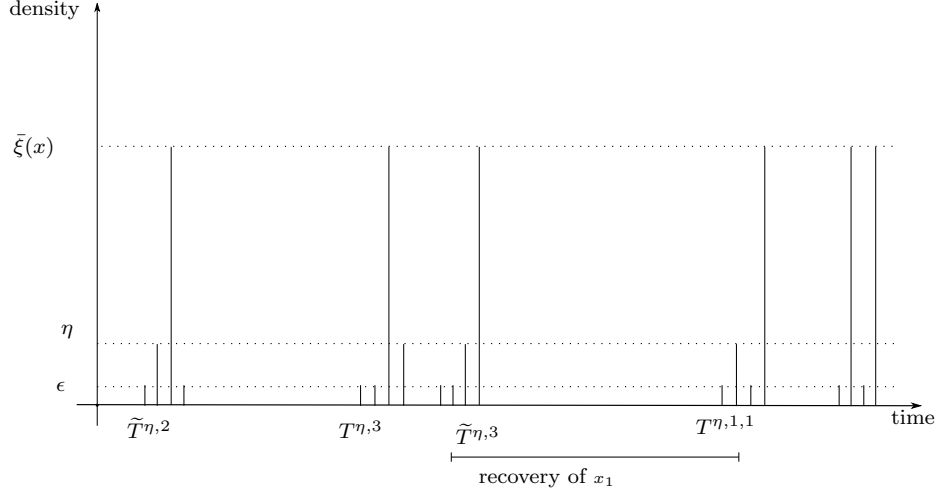
Let $T^{\eta,0}$ and $T^{\eta,3}$ be the first time (resp.) for $\xi_t^\epsilon(x_0)$ and $\xi_t^\epsilon(x_3)$ to reach η -level after $\tilde{T}^{\eta,2}$. Similarly as in the derivation of Eq. (5.21), we get

$$T^{\eta,3} - \tilde{T}^{\eta,2} \sim \frac{1}{f_{3,2}} \ln \frac{1}{\epsilon} \quad (5.33)$$

where $f(\epsilon) \sim g(\epsilon)$ means $\lim_{\epsilon \rightarrow 0} f(\epsilon)/g(\epsilon) = 1$.

Recall from (5.29) that

$$T^{\eta,0} - \tilde{T}^{\eta,2} \sim \frac{-f_{0,1}}{f_{2,1}(b(x_0) - d(x_0))} \ln \frac{1}{\epsilon}. \quad (5.34)$$


 FIGURE 6. Four-type density evolution $(\xi_t^\epsilon(x_0), \xi_t^\epsilon(x_1), \xi_t^\epsilon(x_2), \xi_t^\epsilon(x_3))$

From assumption (C4), one obtains that

$$\frac{-f_{0,1}}{f_{2,1}(b(x_0) - d(x_0))} - \frac{1}{f_{3,2}} > \frac{-f_{1,2}}{f_{3,2}(b(x_1) - d(x_1))} > 0, \quad (5.35)$$

which implies that $T^{\eta,3} < T^{\eta,0}$. Hence, for $t \in [\tilde{T}^{\eta,2}, T^{\eta,3}]$, the population at site x_0 , $\xi_t^\epsilon(x_0)$, stays in some small ϵ -dependent neighborhood of 0. Furthermore, $\xi_t^\epsilon(x_1)$ is influenced mainly from the competition with $\tilde{\xi}(x_2)$. Using comparison arguments as above, one derives that at time $T^{\eta,3}$

$$\begin{aligned} \xi_{T^{\eta,3}}^\epsilon(x_1) &= \xi_{\tilde{T}^{\eta,2}}^\epsilon(x_1) e^{f_{1,2}(T^{\eta,3} - \tilde{T}^{\eta,2})} \\ &\sim \eta e^{f_{1,2} f_{3,2}^{-1} \ln \frac{1}{\epsilon}} \\ &\sim \eta \epsilon^{-\frac{f_{1,2}}{f_{3,2}}}. \end{aligned} \quad (5.36)$$

Similarly as in Step 3, after the time $T^{\eta,3}$, $\xi_t^\epsilon(x_2)$ and $\xi_t^\epsilon(x_3)$ swap their mass in a time of order 1, and $\xi_t^\epsilon(x_2)$ decreases below a level η at time $\tilde{T}^{\eta,3}$. After time $\tilde{T}^{\eta,3}$, $\xi_t^\epsilon(x_1)$ evolves approximately as a logistic growth curve since there is only negligible competition from neighbors x_0, x_2 , i.e.

$$\dot{\xi}_t^\epsilon(x_1) = (b(x_1) - d(x_1) - \alpha(x_1, x_1)\xi_t^\epsilon(x_1))\xi_t^\epsilon(x_1), \quad (5.37)$$

with initial value $\xi_{\tilde{T}^{\eta,3}}^\epsilon(x_1) \sim \eta \epsilon^{-\frac{f_{1,2}}{f_{3,2}}}$.

Denote by $T^{\eta,1,1}$ the second time for the population at site x_1 to increase to the level η . Because of the exponential growth property, as in the derivation of (5.34), one obtains

$$T^{\eta,1,1} - \tilde{T}^{\eta,3} \sim \frac{-f_{1,2}}{f_{3,2}(b(x_1) - d(x_1))} \ln \frac{1}{\epsilon}. \quad (5.38)$$

Comparing the times computed above with the estimate (5.35) on $T^{\eta,0}$, one observes that $T^{\eta,1,1} < T^{\eta,0}$. This means that $\xi_t^\epsilon(x_1)$ recovers to level η faster than $\xi_t^\epsilon(x_0)$ did. Consequently, $\xi_t^\epsilon(x_0)$ will be pushed to 0 due to competition from the fitter type x_1 .

Combining (5.33), (5.38) and the first two equations in (5.30), we obtain the claimed form of the TST limiting configuration (U_t) for $L = 3$. \square

Lemma 5.4. *Assumption (C4) implies the following inequalities, for any $4 \leq L \in \mathbb{N}$*

$$\begin{aligned} \frac{-f_{0,1}}{f_{2,1}(b(x_0) - d(x_0))} &> \frac{1}{f_{3,2}} + \cdots + \frac{1}{f_{L,L-1}}, \\ \frac{-f_{1,2}}{f_{3,2}(b(x_1) - d(x_1))} &> \frac{1}{f_{4,3}} + \cdots + \frac{1}{f_{L,L-1}}, \\ &\vdots \\ \frac{-f_{L-3,L-2}}{f_{L-1,L-2}(b(x_{L-3}) - d(x_{L-3}))} &> \frac{1}{f_{L,L-1}} \end{aligned} \quad (5.39)$$

and

$$\begin{aligned} \frac{-f_{L-4,L-3}}{f_{L-2,L-3}(b(x_{L-4}) - d(x_{L-4}))} - \frac{1}{f_{L-1,L-2}} - \frac{1}{f_{L,L-1}} &> \frac{-f_{L-2,L-1}}{f_{L,L-1}(b(x_{L-2}) - d(x_{L-2}))}, \\ &\vdots \\ \frac{-f_{0,1}}{f_{2,1}(b(x_0) - d(x_0))} - \frac{1}{f_{3,2}} - \frac{1}{f_{4,3}} &> \frac{-f_{2,3}}{f_{4,3}(b(x_2) - d(x_2))} \end{aligned} \quad (5.40)$$

and so on.

The proof of this Lemma follows iterations straightforward from assumption (C4). On the one hand, from (5.39), it implies that when it passes to the limit process U_t , all processes except $\xi_t^\epsilon(x_L)$ stay in ϵ -dependent infinitesimal neighborhoods of 0 at time $T^{\eta,L}$ which denotes the establishing time for type x_L . It leads to monomorphic transportation of the mass from the initial trait x_0 to the fittest trait x_L in the first half period. On the other hand, from (5.40), it guarantees that the fitter one recovers earlier than the unfit traits alternatively backwards to the most unfit one.

Proof of Theorem 3.1. After justifying the form of $(U_t)_{t \geq 0}$ for $L = 2$ in Proposition 5.2 and $L = 3$ in Proposition 5.3, we proceed the proof along two lines, according to whether L is an even or odd integer. We here only prove cases along the line when L is a even integer.

We now deduce the expression for $(U_t)_{t \geq 0}$ when $L = 4$ based on the result for $L = 2$ (see Remark 3.2 (2) and Figure 2).

Based on the analysis in the proof of Proposition 5.3, after time $\tilde{T}^{\eta,3}$, we introduce $T^{\eta,4}$ which is defined as the first time for $\xi_t^\epsilon(x_4)$ to reach the η -level. Similarly as before, we can show that

$$T^{\eta,4} - \tilde{T}^{\eta,3} \sim \frac{1}{f_{4,3}} \ln \frac{1}{\epsilon}. \quad (5.41)$$

Then, after time $T^{\eta,4}$, to mimic Step 3 in the proof of Proposition 5.2, it follows with a selective sweep between subpopulation x_3 and x_4 until time $\tilde{T}^{\eta,4}$ such that $\xi_{\tilde{T}^{\eta,4}}^\epsilon(x_3) = \eta$.

At this stage, $\xi_t^\epsilon(x_2)$ starts to recover due to the lack of competition from $\xi_t^\epsilon(x_3)$. Similarly as in the derivation of (5.38), the time needed for $\xi_t^\epsilon(x_2)$ to again reach the η -level

(denoted by $T^{\eta,2,2}$) can be computed explicitly

$$T^{\eta,2,2} - \tilde{T}^{\eta,4} \sim \frac{-f_{2,3}}{f_{4,3}(b(x_2) - d(x_2))} \ln \frac{1}{\epsilon} =: S_2 \ln \frac{1}{\epsilon} \quad (5.42)$$

which, due to $\tilde{T}^{\eta,4} \sim I_4 \ln \frac{1}{\epsilon}$, implies

$$T^{\eta,2,2} \sim (I_4 + S_2) \ln \frac{1}{\epsilon}. \quad (5.43)$$

After that, it will approach its equilibrium $\bar{\xi}(x_2)$ as a solution of a logistic equation. Consequently, $\xi_t^\epsilon(x_1)$ will drift to 0 due to competition from its fitter neighbor-trait x_2 .

Recall from (5.34) that

$$\begin{aligned} T^{\eta,0} - \tilde{T}^{\eta,4} &\sim \left[\frac{-f_{0,1}}{f_{2,1}(b(x_0) - d(x_0))} - \frac{1}{f_{3,2}} - \frac{1}{f_{4,3}} \right] \ln \frac{1}{\epsilon} \\ &=: (S_0 + I_2 - I_4) \ln \frac{1}{\epsilon} \end{aligned} \quad (5.44)$$

which implies

$$T^{\eta,0} \sim (I_2 + S_0) \ln \frac{1}{\epsilon}. \quad (5.45)$$

Combining the above two estimates (5.42) and (5.44) with assumption (5.40), one observes that

$$T^{\eta,2,2} - \tilde{T}^{\eta,4} < T^{\eta,0} - \tilde{T}^{\eta,4}. \quad (5.46)$$

Moreover, we have

$$\begin{aligned} \lim_{\eta \rightarrow 0} \frac{T^{\eta,2,2}}{\ln \frac{1}{\epsilon}} &= \frac{1}{f_{1,0}} + \frac{1}{f_{2,1}} + \frac{1}{f_{3,2}} + \frac{1}{f_{4,3}} + \frac{|f_{2,3}|}{f_{4,3}(b(x_2) - d(x_2))} \\ &= I_4 + S_2, \end{aligned} \quad (5.47)$$

and

$$\lim_{\eta \rightarrow 0} \frac{T^{\eta,0}}{\ln \frac{1}{\epsilon}} = I_2 + S_0. \quad (5.48)$$

We thus obtain the explicit form of (3.6) for $L = 4$

$$U_t \equiv \begin{cases} \bar{\xi}(x_0)\delta_{x_0} & \text{for } 0 \leq t \leq I_1, \\ \bar{\xi}(x_1)\delta_{x_1} & \text{for } I_1 < t \leq I_2, \\ \bar{\xi}(x_2)\delta_{x_2} & \text{for } I_2 < t \leq I_3, \\ \bar{\xi}(x_3)\delta_{x_3} & \text{for } I_3 < t \leq I_4, \\ \bar{\xi}(x_4)\delta_{x_4} & \text{for } I_4 < t \leq I_4 + S_2, \\ \bar{\xi}(x_2)\delta_{x_2} + \bar{\xi}(x_4)\delta_{x_4} & \text{for } I_4 + S_2 < t \leq I_2 + S_0, \\ \bar{\xi}(x_0)\delta_{x_0} + \bar{\xi}(x_2)\delta_{x_2} + \bar{\xi}(x_4)\delta_{x_4} & \text{for } t > I_2 + S_0 \end{cases} \quad (5.49)$$

which is constructed on top of U_t for $L = 2$ (see (5.2)) by partitioning the interval $(I_2, I_2 + S_0]$ into intervals $(I_2, I_3] \cup (I_3, I_4] \cup (I_4, I_4 + S_2] \cup (I_4 + S_2, I_2 + S_0]$.

To mimic a similar procedure, a TST process for $L = 6$ can be obtained by connecting the TST process for $L = 4$ with a sub-TST consisting of traits $\{x_4, x_5, x_6\}$ specified as in Proposition 5.2.

Recursively, for all even integers L , the form of (3.6) follows. \square

5.2. Proof of Theorem 4.3. To prove the Theorem 4.3, we proceed by listing two key lemmas. In the first one, we conclude that the occurrence time of each successive mutation is asymptotically characterized by exponential distribution while rescaling time in an appropriate way. In the second lemma, we justify that a one-step transition from a current configuration to a new one is in probability one as the migration rate ϵ tends to 0. To avoid repeating arguments, we here only prove the first case of Definition 4.1 while the second one follows a same fashion. The proof is carried out by the method of mathematical induction.

For any non-negative integer l , denote by $\Gamma^{(2l)}$ the atomic measure with finite support, i.e., $\Gamma^{(2l)} = \sum_{i=0}^l \bar{\xi}(x_{2i}^{(2l)}) \delta_{x_{2i}^{(2l)}}$. Similarly, set $\Gamma^{(2l+1)} = \sum_{i=1}^{l+1} \bar{\xi}(x_{2i-1}^{(2l+1)}) \delta_{x_{2i-1}^{(2l+1)}}$, whose form is described as in Definition 4.1. As for the transition from $\Gamma^{(0)}$ to $\Gamma^{(1)}$, it is trivial to be proved as in Proposition 5.2 (a). To the end, it remains to show that the transition rule also holds from configuration $\Gamma^{(2l)}$ to $\Gamma^{(2l+1)}$ for any $l \in \mathbb{N}$. Denote by $\mathbb{P}_{\Gamma^{(2l)}}$ the law of the process $X_t^{\epsilon, \sigma}$ with initial configuration $\Gamma^{(2l)}$. Denote by τ^ϵ the first time after 0 when there occurs a new mutation event.

Lemma 5.5. *Admit the same conditions as in Theorem 4.3.*

$$\lim_{\epsilon \rightarrow 0} \mathbb{P}_{\Gamma^{(2l)}}(\tau^\epsilon > \frac{t}{\sigma}) = \exp\left(-t \sum_{i=0}^l \bar{\xi}(x_{2i}^{(2l)}) \mu(x_{2i}^{(2l)})\right). \quad (5.50)$$

This lemma can be proved in a very similar way as the one for [3, Lemma 2 (c)]. We will not repeat the details here.

Lemma 5.6. *Assume $X_0^{\epsilon, \sigma} = \Gamma^{(2l)} + \rho \delta_{x_{2k}^{(2l)} + h}$. Then, for any $\varepsilon > 0$, there exists a constant $C > 0$ such that*

$$\lim_{\epsilon \rightarrow 0} \mathbb{P}\left(\tau^\epsilon > \ln \frac{1}{\epsilon}, \sup_{t \in (C \ln \frac{1}{\epsilon}, \tau^\epsilon)} \|X_t^{\epsilon, \sigma} - \Gamma^{(2l+1)}\| < \varepsilon\right) = 1 \quad (5.51)$$

where $\Gamma^{(2l+1)}$ is defined as in Definition 4.1 (i), and $\|\cdot\|$ is the total variation norm.

Proof. From Lemma 5.5 and $\frac{1}{\sigma} \gg \ln \frac{1}{\epsilon}$, one concludes that, for any $C > 0$,

$$\lim_{\epsilon \rightarrow 0} \mathbb{P}\left(\tau^\epsilon > C \ln \frac{1}{\epsilon}\right) = 1.$$

According to assumption (D1), there will be one and only one ranked position for the new trait $x_{2k}^{(2l)} + h$ among the supporting traits $\{x_0^{(2l)}, \dots, x_{2j}^{(2l)}, \dots, x_{2l}^{(2l)}\}$ of $\Gamma^{(2l)}$. We will classify two cases according to whether $x_{2k}^{(2l)} + h$ falls on right or left hand side of some $x_{2j}^{(2l)}$ for $0 \leq j \leq l$.

If there exists some $x_{2j}^{(2l)}$ ($0 \leq j \leq l$) such that $x_{2k}^{(2l)} + h$ falls on the right of $x_{2j}^{(2l)}$, one has the local fitness order

$$\dots \prec x_{2j-1}^{(2l)} \prec x_{2j}^{(2l)} \prec x_{2k}^{(2l)} + h \prec x_{2j+1}^{(2l)} \prec \dots \quad (5.52)$$

Since it is unpopulated for both trait sites $x_{2j-1}^{(2l)}$ and $x_{2j+1}^{(2l)}$ at state $\Gamma^{(2l)}$, we consider $(x_{2j}^{(2l)}, x_{2k}^{(2l)} + h)$ as an isolated two-type system because of the assumption of nearest-neighbor competition. By analysis in Lemma 5.1, the population density of this two-type

system converges to $(0, \bar{\xi}(x_{2k}^{(2l)} + h))$ in time of order $O(\ln \frac{1}{\epsilon})$ as $\epsilon \rightarrow 0$. On the right hand side of this pair $(x_{2j}^{(2l)}, x_{2k}^{(2l)} + h)$, the configuration $\sum_{i=j+1}^l \bar{\xi}(x_{2i}^{(2l)})\delta_{x_{2i}^{(2l)}}$ keeps stable as at previous state $\Gamma^{(2l)}$. Whereas on the left hand side of $x_{2j}^{(2l)}$, population density of trait $x_{2j-1}^{(2l)}$, due to the decay of its competitive fitter neighbor trait $x_{2j}^{(2l)}$, recovers exponentially fast upto the stable equilibrium $\bar{\xi}(x_{2j-1}^{(2l)})$ of the following logistic equation

$$\dot{\xi}_t^\epsilon(x_{2j-1}^{(2l)}) = (b(x_{2j-1}^{(2l)}) - d(x_{2j-1}^{(2l)}) - \alpha(x_{2j-1}^{(2l)}, x_{2j-1}^{(2l)})\xi_t^\epsilon(x_{2j-1}^{(2l)}))\xi_t^\epsilon(x_{2j-1}^{(2l)}). \quad (5.53)$$

Continuing in the same way, the mass occupation flips on the left hand side of the trait site $x_{2j}^{(2l)}$ such that traits $\{x_{2i-1}^{(2l)}, 1 \leq i \leq j\}$ get re-established while $\{x_{2i}^{(2l)}, 0 \leq i \leq j\}$ are eliminated. By similar arguments as in the finite trait case (see Section 5.1), the entire rearrangement process can be completed in time of order $O(\ln \frac{1}{\epsilon})$. We obtain the new equilibrium configuration

$$\Gamma^{(2l+1)} = \sum_{i=1}^j \bar{\xi}(x_{2i-1}^{(2l)})\delta_{x_{2i-1}^{(2l)}} + \bar{\xi}(x_{2k}^{(2l)} + h)\delta_{x_{2k}^{(2l)} + h} + \sum_{i=j+1}^l \bar{\xi}(x_{2i}^{(2l)})\delta_{x_{2i}^{(2l)}}. \quad (5.54)$$

In the other case, the fitness location of trait $x_{2k}^{(2l)} + h$ falls on the left hand side of some $x_{2j}^{(2l)}$ for $0 \leq j \leq l$, that is,

$$x_{2j-1}^{(2l)} \prec x_{2k}^{(2l)} + h \prec x_{2j}^{(2l)} \prec x_{2j+1}^{(2l)}.$$

Similarly, consider the sub-populations $(x_{2k}^{(2l)} + h, x_{2j}^{(2l)})$ as an isolated dimorphic system as in Lemma 5.1. Since $\rho \rightarrow 0$ as $\epsilon \rightarrow 0$, we obtain that $(\xi_t(x_{2k}^{(2l)} + h), \xi_t(x_{2j}^{(2l)}))_{t \geq 0}$, starting with $(\rho, \bar{\xi}(x_{2j}^{(2l)}))$, converges to $(0, \bar{\xi}(x_{2j}^{(2l)}))$. Consequently, due to a lack of competition from its nearest fitter neighbor $x_{2k}^{(2l)} + h$, sub-population $x_{2j-1}^{(2l)}$ starts to recover, so does $x_{2i-1}^{(2l)}$ for every $1 \leq i < j$. Thus, we obtain the new equilibrium configuration

$$\Gamma^{(2l+1)} = \sum_{i=1}^j \bar{\xi}(x_{2i-1}^{(2l)})\delta_{x_{2i-1}^{(2l)}} + \sum_{i=j}^l \bar{\xi}(x_{2i}^{(2l)})\delta_{x_{2i}^{(2l)}}.$$

In conclusion, the new configuration $\Gamma^{(2l+1)}$ is obtained by relabeling the traits as done in Definition 4.1 (i). \square

Lemma 5.5, shows that the mutation occurs on the time scale $O(\frac{1}{\sigma})$. Recall from Section 3 that the time scale for fixation is $O(\ln \frac{1}{\epsilon})$ on a finite trait space. Combining them with the time scale separation constraint $\frac{1}{\sigma} \gg \ln \frac{1}{\epsilon}$ (heuristically introduced by Metz et al [17] and mathematically developed by Champagnat [3]), the proof of Theorem 4.3 is as follows.

Proof of Theorem 4.3. For any non-negative $L \in \mathbb{N}$, let $B^{(L)}$ be a measurable subset of \mathcal{X}^L , such that $B^{(L)} := \{\mathbf{x}^{(L)} = (x_0^{(L)}, \dots, x_L^{(L)}) : x_0^{(L)} \prec \dots \prec x_L^{(L)}\}$ as in Assumption (D1).

Define, for any $L = 2l$ even,

$$\bar{n}(x_i^{(L)}) = \begin{cases} \bar{\xi}(x_i^{(L)}) & \text{for } i \text{ even integer} \\ 0 & \text{for } i \text{ odd integer,} \end{cases} \quad (5.55)$$

and for $L = 2l + 1$ odd,

$$\bar{n}(x_i^{(L)}) = \begin{cases} 0 & \text{for } i \text{ even integer} \\ \bar{\xi}(x_i^{(L)}) & \text{for } i \text{ odd integer.} \end{cases} \quad (5.56)$$

Then the support process of $(\Gamma_t)_{t \geq 0}$ in Definition 4.1, denoted by $(Z_t)_{t \geq 0}$, has the following infinitesimal generator

$$G\varphi(\mathbf{x}^{(L)}) = \int_{\mathbb{R}^d} (\varphi(\mathbf{x}^{(L+1)}) - \varphi(\mathbf{x}^{(L)})) \beta(\mathbf{x}^{(L)}) \kappa(\mathbf{x}^{(L)}, dh), \quad (5.57)$$

where $\beta(\mathbf{x}^{(L)}) = \sum_{i=0}^L \bar{n}(x_i^{(L)}) \mu(x_i^{(L)})$, and the probability kernel

$$\kappa(\mathbf{x}^{(L)}, dh) = \sum_{k=0}^L \frac{\bar{n}(x_k^{(L)}) \mu(x_k^{(L)})}{\beta(\mathbf{x}^{(L)})} p(x_k^{(L)}, dh), \quad (5.58)$$

and $\mathbf{x}^{(L+1)} = (x_1^{(L+1)}, \dots, x_{L+1}^{(L+1)})$ is determined by $\mathbf{x}^{(L)}$ and $p(x_k^{(L)}, dh)$ as in Definition 4.1.

According to Definition 4.1, let $P_{\mathbf{x}^{(L)}}$ be the law of $(Z_t)_{t \geq 0}$ with initial state $\mathbf{x}^{(L)}$. Denote by $(S_n)_{n \geq 1}$ the sequence of occurrence times of mutations. By applying the strong Markov property at S_1 , we obtain

$$\begin{aligned} & P_{\mathbf{x}^{(L)}}(S_n < t < S_{n+1}, Z_t \in B^{(L+n)}) \\ &= \int_0^t \beta(\mathbf{x}^{(L)}) \exp^{-s\beta(\mathbf{x}^{(L)})} \int_{h \in \mathbb{R}^d} P_{\mathbf{x}^{(L+1)}}(S_{n-1} < t-s < S_n, Z_{t-s} \in B^{(L+n)}) \kappa(\mathbf{x}^{(L)}, dh) ds. \end{aligned} \quad (5.59)$$

In particular,

$$P_{\mathbf{x}^{(L)}}(0 \leq t < S_1, Z_t \in B^{(L)}) = 1_{\{\mathbf{x}^{(L)} \in B^{(L)}\}} \exp(-t\beta(\mathbf{x}^{(L)})). \quad (5.60)$$

The idea of our proof for the theorem is to show that the same relation as above holds for the rescaled processes $(X_{t/\sigma}^{\epsilon, \sigma})_{t \geq 0}$ as taking $\epsilon \rightarrow 0$ when we replace Z_t by $\text{Supp}(X_{t/\sigma}^{\epsilon, \sigma})$ and replace S_n by the n -th jump time τ_n^ϵ of $(X_{t/\sigma}^{\epsilon, \sigma})_{t \geq 0}$.

Let $\mathbb{P}_{\mathbf{x}^{(L)}}$ be the law of $(X_{t/\sigma}^{\epsilon, \sigma})_{t \geq 0}$ with initial state's support $\mathbf{x}^{(L)}$. Consider the quantity

$$\mathbb{P}_{\mathbf{x}^{(L)}}(\tau_n^\epsilon < t < \tau_{n+1}^\epsilon, \text{Supp}(X_{t/\sigma}^{\epsilon, \sigma}) \in B^{(L+n)}). \quad (5.61)$$

For $n = 0$, it is implied from Lemma 5.5 that

$$\lim_{\epsilon \rightarrow 0} \mathbb{P}_{\mathbf{x}^{(L)}}(0 \leq t < \tau_1^\epsilon, \text{Supp}(X_{t/\sigma}^{\epsilon, \sigma}) \in B^{(L)}) = 1_{\{\mathbf{x}^{(L)} \in B^{(L)}\}} \exp(-t\beta(\mathbf{x}^{(L)})). \quad (5.62)$$

For $n \geq 1$, by the strong Markov property at τ_1^ϵ , we obtain

$$\begin{aligned} & \mathbb{P}_{\mathbf{x}^{(L)}} \left(\tau_n^\epsilon < t < \tau_{n+1}^\epsilon, \text{Supp}(X_{t/\sigma}^{\epsilon, \sigma}) \in B^{(L+n)} \right) \\ &= \mathbb{P}_{\mathbf{x}^{(L)}} (\tau_1^\epsilon < t) \int_{h \in \mathbb{R}^d} \mathbb{P}_{\mathbf{x}^{(L+1)}} \left(\tau_{n-1}^\epsilon < t - \tau_1^\epsilon < \tau_n^\epsilon, \text{Supp}(X_{\frac{t-\tau_1^\epsilon}{\sigma}}^{\epsilon, \sigma}) \in B^{(L+n)} \right) \kappa^\epsilon(\mathbf{x}^{(L)}, dh) \end{aligned} \quad (5.63)$$

where $\kappa^\epsilon(\mathbf{x}^{(L)}, dh) = \frac{\sum_{k=0}^L \xi_{\tau_1^\epsilon}^\epsilon(x_k^{(L)}) \mu(x_k^{(L)}) p(x_k^{(L)}, dh)}{\sum_{k=0}^L \xi_{\tau_1^\epsilon}^\epsilon(x_k^{(L)}) \mu(x_k^{(L)})}$ converges to $\frac{\sum_{k=0}^L \bar{n}(x_k^{(L)}) \mu(x_k^{(L)}) p(x_k^{(L)}, dh)}{\sum_{k=0}^L \bar{n}(x_k^{(L)}) \mu(x_k^{(L)})}$ as $\epsilon \rightarrow 0$

due to Theorem 3.1 and the form of $\bar{n}(\cdot)$ given in Eq.(5.55) and (5.56).

Substituting the terms on the RHS of Eq.(5.63) by their limits when taking $\epsilon \rightarrow 0$, combining with (5.62) and (5.58), we obtain

$$\begin{aligned} & \lim_{\epsilon \rightarrow 0} \mathbb{P}_{\mathbf{x}^{(L)}} \left(\tau_n^\epsilon < t < \tau_{n+1}^\epsilon, \text{Supp}(X_{t/\sigma}^{\epsilon, \sigma}) \in B^{(L+n)} \right) \\ &= \lim_{\epsilon \rightarrow 0} \int_0^t \beta(\mathbf{x}^{(L)}) \exp(-s\beta(\mathbf{x}^{(L)})) \int_{h \in \mathbb{R}^d} \sum_{k=0}^L \frac{\bar{n}(x_k^{(L)}) \mu(x_k^{(L)}) p(x_k^{(L)}, dh)}{\sum_{k=0}^L \bar{n}(x_k^{(L)}) \mu(x_k^{(L)})} \\ & \quad \cdot \mathbb{P}_{\mathbf{x}^{(L+1)}} \left(\tau_{n-1}^\epsilon < t - s < \tau_n^\epsilon, \text{Supp}(X_{\frac{t-s}{\sigma}}^{\epsilon, \sigma}) \in B^{(L+n)} \right) ds \\ &= \int_0^t \beta(\mathbf{x}^{(L)}) \exp(-s\beta(\mathbf{x}^{(L)})) \\ & \quad \int_{h \in \mathbb{R}^d} \lim_{\epsilon \rightarrow 0} \mathbb{P}_{\mathbf{x}^{(L+1)}} \left(\tau_{n-1}^\epsilon < t - s < \tau_n^\epsilon, \text{Supp}(X_{\frac{t-s}{\sigma}}^{\epsilon, \sigma}) \in B^{(L+n)} \right) \kappa(\mathbf{x}^{(L)}, dh) ds. \end{aligned} \quad (5.64)$$

By (5.60) and (5.62), we conclude that

$$\lim_{\epsilon \rightarrow 0} \mathbb{P}_{\mathbf{x}^{(L)}} \left(0 \leq t < \tau_1^\epsilon, \text{Supp}(X_{t/\sigma}^{\epsilon, \sigma}) \in B^{(L)} \right) = P_{\mathbf{x}^{(L)}} (0 \leq t < S_1, Z_t \in B^{(L)}), \quad (5.65)$$

and moreover, by (5.59) and (5.64), we conclude that

$$\lim_{\epsilon \rightarrow 0} \mathbb{P}_{\mathbf{x}^{(L)}} \left(\tau_n^\epsilon < t < \tau_{n+1}^\epsilon, \text{Supp}(X_{t/\sigma}^{\epsilon, \sigma}) \in B^{(L+n)} \right) = P_{\mathbf{x}^{(L)}} (S_n < t < S_{n+1}, Z_t \in B^{(L+n)}). \quad (5.66)$$

Thus, by conditional probability and Lemma 5.6, for any $\varepsilon > 0$

$$\begin{aligned} & \lim_{\epsilon \rightarrow 0} \mathbb{P}_{\mathbf{x}^{(L)}} \left(\tau_n^\epsilon < t < \tau_{n+1}^\epsilon, \text{Supp}(X_{t/\sigma}^{\epsilon, \sigma}) \in B^{(L+n)}, \|X_{t/\sigma}^{\epsilon, \sigma} - \Gamma^{(L+n)}\| < \varepsilon \right) \\ &= \lim_{\epsilon \rightarrow 0} \mathbb{P}_{\mathbf{x}^{(L)}} \left(\tau_n^\epsilon < t < \tau_{n+1}^\epsilon, \text{Supp}(X_{t/\sigma}^{\epsilon, \sigma}) \in B^{(L+n)} \right) \mathbb{P}_{\mathbf{x}^{(L+n)}} \left(\|X_{t/\sigma}^{\epsilon, \sigma} - \Gamma^{(L+n)}\| < \varepsilon \right) \\ &= P_{\mathbf{x}^{(L)}} (S_n < t < S_{n+1}, Z_t \in B^{(L+n)}). \end{aligned} \quad (5.67)$$

Therefore, Theorem 4.3 is proved in the sense of one-dimensional time marginal distribution. It can be generalized to convergence in finite dimensional distribution similarly as in [3]. \square

6. SIMULATION ALGORITHM

The pathwise construction of the TST process defined in Definition 4.1 leads to the following numerical algorithm for simulation of the TST process.

Step 0. Specify the initial condition: $\Gamma_0 = \Gamma^{(0)} = \bar{\xi}(x_0)\delta_{x_0}$.

Step 1. Simulate τ_1 exponential distributed with parameter $\bar{\xi}(x_0)\mu(x_0)$. Sample a new trait (x_0+h) with density $p(x_0, dh)$. If $f(x_0+h, x_0) > 0$, relabel $x_0^{(1)} := x_0$, $x_1^{(1)} := x_0+h$. Otherwise, relabel $x_0^{(1)} := x_0+h$, $x_1^{(1)} := x_0$. Set $\Gamma^{(1)} = \bar{\xi}(x_1^{(1)})\delta_{x_1^{(1)}}$, and $\Gamma_t = \Gamma^{(0)}$ for $t \in [0, \tau_1)$.

Step 2. Simulate τ_2 exponential distributed with parameter $\bar{\xi}(x_1^{(1)})\mu(x_1^{(1)})$.

Set $\Gamma_t = \Gamma^{(1)}$ for $t \in [\tau_1, \tau_1 + \tau_2)$.

Sample a new trait $(x_1^{(1)}+h)$ with density $p(x_1^{(1)}, dh)$.

Choose one from the following to carry out:

- if $f(x_1^{(1)}+h, x_1^{(1)}) > 0$, relabel $x_0^{(2)} := x_0^{(1)}$, $x_1^{(2)} := x_1^{(1)}$, $x_2^{(2)} := x_1^{(1)}+h$;
- if $f(x_1^{(1)}+h, x_1^{(1)}) < 0$, $f(x_1^{(1)}+h, x_0^{(1)}) > 0$, relabel $x_0^{(2)} := x_0^{(1)}$, $x_1^{(2)} := x_1^{(1)}+h$, $x_2^{(2)} := x_1^{(1)}$;
- if $f(x_1^{(1)}+h, x_0^{(1)}) < 0$, relabel $x_0^{(2)} := x_1^{(1)}+h$, $x_1^{(2)} := x_0^{(1)}$, $x_2^{(2)} := x_1^{(1)}$.

Set $\Gamma^{(2)} = \bar{\xi}(x_0^{(2)})\delta_{x_0^{(2)}} + \bar{\xi}(x_2^{(2)})\delta_{x_2^{(2)}}$.

Step $2l+1$. Generate $\Gamma^{(2l+1)}$ from $\Gamma^{(2l)} = \sum_{i=0}^l \bar{\xi}(x_{2i}^{(2l)})\delta_{x_{2i}^{(2l)}}$ for $l = 1, 2, \dots$.

Simulate τ_{2l+1} exponential distributed with parameter $\sum_{i=0}^l \bar{\xi}(x_{2i}^{(2l)})\mu(x_{2i}^{(2l)})$.

Set $\Gamma_t = \Gamma^{(2l)}$ for $t \in [\sum_{i=1}^{2l} \tau_i, \sum_{i=1}^{2l+1} \tau_i)$. Select one trait $x_{2k}^{(2l)}$, for any $0 \leq k \leq l$,

to mutate with probability $\frac{\bar{\xi}(x_{2k}^{(2l)})\mu(x_{2k}^{(2l)})}{\sum_{i=0}^l \bar{\xi}(x_{2i}^{(2l)})\mu(x_{2i}^{(2l)})}$. Sample a new trait $(x_{2k}^{(2l)}+h)$ with probability density $p(x_{2k}^{(2l)}, dh)$. Choose one from the following three cases to carry out:

- if $f(x_{2k}^{(2l)}+h, x_{2l}^{(2l)}) > 0$, relabel $x_{2l+1}^{(2l+1)} := x_{2k}^{(2l)}+h$, $x_i^{(2l+1)} := x_i^{(2l)}$ for $0 \leq i \leq 2l$;
- if $f(x_{2k}^{(2l)}+h, x_0^{(2l)}) < 0$, relabel $x_i^{(2l+1)} := x_{i-1}^{(2l)}$ for $1 \leq i \leq 2l+1$, and $x_0^{(2l+1)} := x_{2k}^{(2l)}+h$;
- otherwise, there exists $0 \leq j < l$ s.t. $f(x_{2k}^{(2l)}+h, x_{2i}^{(2l)}) < 0$ for $j < i \leq l$, and $f(x_{2k}^{(2l)}+h, x_{2j}^{(2l)}) > 0$. Furthermore,
 - * if $f(x_{2k}^{(2l)}+h, x_{2j+1}^{(2l)}) < 0$, relabel $x_i^{(2l+1)} := x_i^{(2l)}$ for $0 \leq i \leq 2j$, $x_i^{(2l+1)} := x_{i-1}^{(2l)}$ for $2j+2 \leq i \leq 2l+1$, and $x_{2j+1}^{(2l+1)} := x_{2k}^{(2l)}+h$;
 - * if $f(x_{2k}^{(2l)}+h, x_{2j+1}^{(2l)}) > 0$, relabel $x_i^{(2l+1)} := x_i^{(2l)}$ for $0 \leq i \leq 2j+1$, $x_i^{(2l+1)} := x_{i-1}^{(2l)}$ for $2j+3 \leq i \leq 2l+1$, and $x_{2j+2}^{(2l+1)} := x_{2k}^{(2l)}+h$.

Set $\Gamma^{(2l+1)} = \sum_{i=1}^{l+1} \bar{\xi}(x_{2i-1}^{(2l+1)})\delta_{x_{2i-1}^{(2l+1)}}$.

Step 2l+2. To generate $\Gamma^{(2l+2)}$ from $\Gamma^{(2l+1)} = \sum_{i=1}^{l+1} \bar{\xi}(x_{2i-1}^{(2l+1)}) \delta_{x_{2i-1}^{(2l+1)}}$ for $l = 1, 2, \dots$.

This can be done as similar as the induction from $\Gamma^{(2l)}$ to $\Gamma^{(2l+1)}$. So forth.

APPENDIX A. STABILITY OF A LOTKA-VOLTERRA SYSTEM

Consider a Lotka-Volterra system $(n(x), n(y))$ satisfying the following equations.

$$\begin{cases} \dot{n}_t(x) = (b(x) - d(x) - \alpha(x, x)n_t(x) - \alpha(x, y)n_t(y)) n_t(x) \\ \dot{n}_t(y) = (b(y) - d(y) - \alpha(y, x)n_t(x) - \alpha(y, y)n_t(y)) n_t(y). \end{cases} \quad (\text{A.1})$$

Suppose that $n_0(x), n_0(y) > 0$ and $f(y, x) := b(y) - d(y) - \alpha(y, x)\bar{n}(x) > 0$, $\bar{n}(x) = \frac{b(x)-d(x)}{\alpha(x, x)}$, and its symmetric form $f(x, y) < 0$. Then we conclude that $(0, \bar{n}(y))$ is the only stable point.

In fact, there are four fixed points of above system, namely, $(0, 0)$, $(\bar{n}(x), 0)$, $(0, \bar{n}(y))$, and $(n^*(x), n^*(y))$, where $(n^*(x), n^*(y))$ is such that

$$\begin{cases} b(x) - d(x) - \alpha(x, x)n_t(x) - \alpha(x, y)n_t(y) = 0 \\ b(y) - d(y) - \alpha(y, x)n_t(x) - \alpha(y, y)n_t(y) = 0. \end{cases}$$

By simple calculation, we obtain that

$$\begin{cases} n^*(x) = \frac{\alpha(y, y)f(x, y)}{\alpha(x, x)\alpha(y, y) - \alpha(x, y)\alpha(y, x)} \\ n^*(y) = \frac{\alpha(x, x)f(y, x)}{\alpha(x, x)\alpha(y, y) - \alpha(x, y)\alpha(y, x)}. \end{cases}$$

To make sense of the solution as a population density (which must be non-negative), one needs $f(x, y) \cdot f(y, x) > 0$. It contradicts the assumption $f(x, y) < 0, f(y, x) > 0$. We thus exclude the solution $(n^*(x), n^*(y))$.

The Jacobian matrix for the system (A.1) at point $(0, 0)$ is

$$\begin{pmatrix} b(x) - d(x) & 0 \\ 0 & b(y) - d(y) \end{pmatrix}.$$

Obviously its eigenvalues are both positive. Thus $(0, 0)$ is unstable.

The Jacobian matrix at point $(\bar{n}(x), 0)$ is

$$\begin{aligned} & \begin{pmatrix} -(b(x) - d(x)) & -\alpha(x, y)\bar{n}(x) \\ 0 & b(y) - d(y) - \alpha(y, x)\bar{n}(x) \end{pmatrix} \\ &= \begin{pmatrix} -(b(x) - d(x)) & -\alpha(x, y)\bar{n}(x) \\ 0 & f(y, x) \end{pmatrix}. \end{aligned}$$

Since one of its eigenvalue $-(b(x) - d(x))$ is negative whereas the other one is $f(y, x) > 0$, the equilibrium $(\bar{n}(x), 0)$ is unstable.

The Jacobian matrix of system (A.1) at point $(0, \bar{n}(y))$ is

$$\begin{pmatrix} b(x) - d(x) - \alpha(x, y)\bar{n}(y) & 0 \\ -\alpha(y, x)\bar{n}(y) & -(b(y) - d(y)) \end{pmatrix} = \begin{pmatrix} f(x, y) & 0 \\ -\alpha(y, x)\bar{n}(y) & -(b(y) - d(y)) \end{pmatrix},$$

whose eigenvalues are both negative because of the condition $f(x, y) < 0$. Thus $(0, \bar{n}(y))$ is the only stable equilibrium of the system (A.1).

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